INHERITANCE OF COLD RESISTANCE AND OTHER CHARACTERS IN THE BACKCROSS, KANRED x KANMARQ

by

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INTRODUCTION

The object of this backcross was to try to combine the excellent grain quality, stiffness of straw and earliness of Kanmarq with the desirable characters of Kanred, especially winterhardiness. The backcross method is believed to be especially useful in solving a problem of this sort, where the plant breeder wants to introduce additional factors for a given character, such as winterhardiness, to the cross from the hardy parent. In crosses where the characters desired are quantitatively inherited, and the exact genetic ratios are not known, the use of the adapted variety as one parent and its offspring as the other seems to be a promising method of crop improvement.

From this cross it appears that it should be possible to produce a new variety adapted to Kansas that has the winterhardiness of Kanred, and the stiff straw, earliness and quality of Kanmarq. The object in this paper is not to determine the most promising hybrid strain with respect to such agronomic characters as yield, stiffness of straw, etc. It would be beyond reason to expect that such characters, which are quantitatively inherited could be isolated in homozygous condition in the fourth generation. It is believed, however, that the F_3 and F_4 hybrid

lines tested differ in regard to quality, winterhardiness, earliness, etc., and it is these differences that are described in this paper.

REVIEW OF LITERATURE

Winterhardiness

Clark, Martin and Parker (7) state that the winterkilling in wheat over a period of fourteen years has caused an average loss of 3.5 per cent. This is about equal to the loss due to wheat diseases. The extent of abandonment varies from one to twenty-nine per cent annually, with an average of about ten per cent for the period, 1901-1923. Not all of these losses are due to winterkilling. Soil blowing, Hessian fly, drouth, and other factors are also involved.

Hill and Salmon (12) believe the problem of winterhardiness to be very important and one deserving serious attention. Varieties of winter wheat that are of inferior quality are now being grown in certain regions due to their ability to survive cold winters. They believe winterhardiness depends on the ability of a plant to build up a high degree of protection against cold. This process is commonly known as hardening off. Kanred belongs to that

class of winter wheat which is relatively hardy either in the hardened or unhardened condition.

Newton (15) found a direct relation between the imbibition pressure of fresh leaves of wheat and their winterhardiness. The amount of juice that could be obtained from 100 grams of leaves was negatively correlated with hardiness. Unhardened material does not show these relations.

Newton and Brown (16) state that the moisture content is the most important factor causing certain wheat varieties to be hardy. The resulting concentration of the colloids and sugars increases the resistance to freezing.

Martin (13) found that the hardy wheats contained sap of higher concentration, higher osmotic pressure, a larger per cent of bound water, and a lower transpiration rate. He is of the opinion that varieties differ in these respects and that the same varieties differ under different growing conditions. Martin found that winterhardiness in hybrids in general was intermediate between the parents, with occasional transgressive segregation.

Maximov (14) attributes winterkilling to one of two causes, (a) the increased concentration of the cell sap when water is withdrawn by freezing causes a chemical reaction that kills the protoplasm; (b) a crushing of the cells caused by ice crystals forming in the intercellular

spaces. He believes the second cause to be responsible for most of the freezing injury. Maximov states that Muller and Thurgau in 1882, discovered that there was an accumulation of sugar with a decrease in temperature. No correlation between sugar content and cold resistance could be found unless the varieties were studied at the time of the coldest temperatures.

Nilsson-Ehle, Hayes and Garber, Gaines and others believe that winterhardiness is quantitatively inherited, but the genetic factors involved have not been determined.

Hayes and Aamodt (10), in a study of the first four generations of the cross Marquis x Minhardi and Marquis x Minturki, found that cold resistance behaves as a recessive character. Cold resistance and winter habit were strongly correlated, but the correlation was not absolute.

Apparently it is possible to obtain spring wheats which are as hardy as the most winter-resistant varieties. There was no significant positive correlation between the winterhardiness of the same hybrid lines in the F_3 and F_4 generations. This result would be expected due to the many factors, environmental as well as genetic, which affect winterhardiness.

Quisenberry and Clark (17), in a study of numerous wheat crosses made for winterhardiness studies, conclude

that winterhardiness is a heritable character but of a very complex nature and that it is greatly influenced by environment. They did not attempt any genetic explanation of the inheritance of winterhardiness. The value of freezing tests under controlled conditions to compare with field tests, is appreciated by these authors.

Akerman (1) considers that plant breeders who are studying genetic material, can use the rapid method of testing for frost resistance in refrigeration chambers instead of relying on field tests as the only measure of cold resistance.

Quality

Shollenberger and Clark (19) in a study made of the milling and baking qualities of American wheat varieties concluded that new and standard varieties differ greatly in their quality. It is their opinion that yield alone does not justify the distribution of a new wheat. It must also have qualities that are satisfactory to the miller and baker.

Alsberg (2) expresses the same opinion in a summary of the objectives of wheat breeding when he states that "a balance of desirable characters is necessary. The economic aspects now important are the outgrowth of a long evolution in agriculture, milling, baking and standards of

living."

Swanson (20) has theoretically pictured and described the structure of the starch and protein molecules in flour, based on their behavior in bread making. The starch molecules are round, and the protein molecules fibrous in nature. Strength in dough is due to the adhesion of the strands of the protein molecules. Excess working, use of shortening, and the inherent characteristics of these protein molecules constitute the strength and nature of flour.

Hayes, Immer, and Bailey (11) made a study of the relation between baking quality and a number of agronomic and grain characters in wheat. They conclude that at present there is no assurance of being able to select good quality hybrids on the basis of any grain or agronomic character. Plant breeders at present can only select for kernel types that meet the grain grading standards. Quality determinations must be made when the hybrids are increased to the extent of producing enough grain for experimental milling and baking tests. This requires from 1000 to 2000 grams.

Clark (4) states that crude protein content in hybrids of Marquis x Hard Federation and Hard Federation x Propo is quantitatively inherited in as complex a manner as yield, and is affected by environment equally as much as

yield. Some high protein F_3 strains were obtained from selecting F_2 plants producing grain of high protein content, but not all superior F_2 plants gave high protein strains in F_3. Strains of higher protein content than the high protein parent were not obtained.

Clark and Quisenberry (8) found that the average crude protein content of the F_2 plants and F_3 strains in a Marquis x Kota cross was not significantly different from that of the low protein Marquis parent. F_2 plants and F_3 strains of lower protein content than the low protein parent were obtained. No strains of higher protein content than the high protein parent were obtained. The crude protein content of F_2 plants and F_3 strains was positively correlated. Those results indicate that in breeding for high protein content that selection of high protein plants in the segregating F_2 generation offers a promising method of attack.

Clark (3) in a study of the cross, Kota x Hard Federation, found that the F_4 hybrids averaged slightly higher in protein content than either parent. The variability of the F_4 crosses indicated that there was segregation for protein content.

Clark and Ausemus (6) reported some results on inheritance of protein content in crosses between Hope wheat and

other varieties. These investigators found that the F_3 hybrids were mostly intermediate in protein content, although the differences between the parents and the crosses were not wide. Plants were obtained that exceeded the limits of the low and high protein parents in protein content.

MATERIALS AND METHODS

The Kanred x Kanmarq cross used in this study was made in 1923 by Mr. B. B. Bayles, at the Kansas Agricultural Experiment Station. The F_1 plants were grown in the greenhouse at Manhattan, Kansas, during the winter of 1924 and 1925. The F_2 crop of this cross was grown at Davis, California, by Mr. V. H. Florell, during the winter of 1926-1927. The studies of the various characters mentioned in this paper were made on the F_3 and F_4 generations grown during the years 1927-1928 and 1928-1929.

The variety Kanred, as reported by Salmon (18) and Clark and Salmon (9) is a selection from Crimean wheat developed at the Kansas Agricultural Experiment Station. Kanred closely resembles the Turkey and Kharkov varieties, the outstanding distinguishing feature being the long beaks found on Kanred. The Kanred beaks vary from five to twenty mm. in length, depending on the ecological conditions under which the plant develops. Kanred has out-

yielded Turkey and Kharkov about three bushels per acre over a ten-year period in Kansas. Kanred is slightly more winterhardy than Turkey and Kharkov and is resistant to certain forms of black stem rust. Kanred is now grown on about one million acres in Kansas. The very weak straw of Kanred is its most undesirable character.

The variety Kanmarq is a selection from a Kanred x Marquis cross. The Marquis parent is an excellent quality spring wheat and occupies much of the spring wheat area in the northern United States and Canada. Kanmarq has glabrous white glumes, and is awnless. The grain quality of Kanmarq appears to be equal to that of Marquis. The kernels of Kanmarq are similar to Marquis, and are shorter than those of Kanred. Kanmarq has stiffer straw and is earlier than Kanred. The most objectionable feature of Kanmarq is its relatively low degree of cold resistance. The fact that Kanmarq is beardless is probably a disadvantage because it is known that the awns of wheat perform some role in kernel development that tends to make bearded varieties yield more than awnless sorts in dry climates such as found in Kansas. Kanmarq is not grown commercially on farms at the present time and will probably never be distributed.

A summary of the agronomic data on Kanred and Kanmarq grown in the crop improvement nursery, Manhattan, Kansas, during the eight-year period, 1922-1929, inclusive, is given in Table I. As can be seen, the two varieties do not differ very widely in their agronomic characters. Kanmarq is slightly earlier, has stiffer straw and is more resistant to leaf rust than Kanred.

The data on grain characters of Kanred and Kanmarq grown in the crop improvement nursery during the eight-year period, 1922-1929, are summarized in Table II. Kanmarq produced plumper grain, of higher test weight, than Kanred. The protein content, based on an average of three years' results, is about one per cent higher for Kanred. This difference in protein content is in accord with the known negative correlation between plumpness or test weight of grain and protein content.

A similar study was made of these two varieties grown in plots at the Agronomy Farm for the period 1924 to 1928, inclusive. The yield data are presented in Table III.

Table I . Summary of agronomic data on Kanred(Ka) and Kanmarq(Kq) grown in the Agronomy nursery, Manhattan, Kansas, 1922 - 1929.

Year	Height of Plant (Inches)		% Lodging		% Leaf rust		Date fully headed (May)		Date ripe (June)		Yield, bu. per acre	
	Ka.	Kq.	Ka.	Kq.	Ka.	Kq.	Ka.	Kq.	Ka.	Kq.	Ka.	Kq.
1922	50	49	--	--	--	--	26	25	22	21	46.9	49.9
1923	44	44	--	--	15	tr	28	27	27	28	37.1	45.9
1924	27	26	--	--	--	--	29	29	25	25	14.8	13.5
1925	39	37	50	0	20	5	19	19	16	16	32.9	24.8
1926	39	37	--	--	--	--	26	25	16	16	35.4	26.5
1927	--	--	73	67	80	33	27	24	28	28	20.7	27.5
1928	37	37	65	11	58	32	24	25	28	26	49.3	52.9
1929	48	48	90	80	43	5	28	26	26	26	20.0	30.0
Ave.	40.6(a)	39.7[illegible]	70(b)	40	43(c)	15	26	25	24	23	32.1	33.9

(a) 7 years
(b) 4 years
(c) 5 years

Table II . Summary of data on yield and grain quality of Kanred(Ka) and Kanmarq(Kq) grown in the Agronomy Nursery, Manhattan, Kansas. 1922-1929.

Year	Yield Bu. per Acre		Test Weight Pounds		% Plumpness of Kernèls		% Yellow berry		% Protein content	
	Ka.	Kq.	Ka.	Kq.	Ka.	Kq.	Ka.	Kq.	Ka.	Kq.
1922	46.9	49.9	59.1	59.3	88	88	38	25	-----	---
1923	37.1	45.8	56.4	59.4	68	81	3	6	15.39	13.51
1924	14.8	13.5	59.8	58.5	87	85	90	85	-----	-----
1925	32.9	24.8	59.7	60.2	83	82	0	0	-----	-----
1926	34.5	26.5	57.1	53.8	83	78	0	0	-----	-----
1927	20.7	27.5	----	----	72	85	0	5	15.72	15.30
1928	49.3	52.9	59.5	60.5	84	90	8	2	14.45	13.60
1929	20.0	30.0	47.9	56.7	60	83	0	2	-----	-----
Ave.	32.1	33.9	57.1(a)	58.3	78	84	17	16	15.19	*14.14

(a) seven year average
* Three year average.

Table III. Yields of Kanred and Kanmarq grown in plots at the Agronomy Farm, Manhattan, Kansas, 1924-1928

Year	Yield - bushels per acre	
	Kanred	Kanmarq
1924	34.0	30.8
1925	39.0	35.6
1926	29.6	33.6
1927	35.5	43.0
1928	46.4	46.5
Averages	36.9	37.9

The slightly higher yield of Kanmarq is probably not highly significant. In two of the five years, Kanred outyielded Kanmarq. The reverse is true for two other seasons. In one year the yields of the two varieties were almost the same.

A summary of the milling and baking tests on the grain of Kanred and Kanmarq produced in plots at the Agronomy Farm for the years 1924 to 1928 is given in Table IV. These tests were made by the Department of Milling Industry at the Kansas State Agricultural College. The test weight, protein content, and flour yield of the two varieties differ only slightly. However, it appears that Kanmarq is better than Kanred as a bread-making wheat, since it produces a loaf of superior volume,

Table IV. Milling and baking tests of Kanred(Ka) and Kanmarq(Kq) grown in plots at the Agronomy Farm, Manhattan, Kansas. 1924-1928.

Year	Test Weight Pounds		% Prot. in wheat		% Flour yield		Loaf volume c c		Loaf Texture score		Loaf color score	
	Ka.	Kq.	Ka.	Kq.	Ka.	Kq.	Ka.	Kq.	Ka.	Kq.	Ka.	Kq.
1924	62.1	61.3	12.60	12.70	73.5	73.0	1935	1855*	95	94	92	92
1925	61.5	61.8	11.80	11.90	71.5	70.7	1970	2090	98	98	99	99
1926	57.3	57.9	13.40	13.00	68.5	67.5	2040	2160	97	98	96	98
1927	59.3	61.3	12.60	12.75	70.1	70.5	1930	1980	95	96	97	97
1928	61.2	61.7	11.40	10.80	69.0	70.0	1980	2075	97	98	98	99
Ave.	60.3	60.8	12.56	12.24	70.5	70.3	1971	2032	96	97	96	97

* Gentle method used in 1924.

texture and color. Attention is called to the fact that in 1924 Kanmarq produced a loaf of less volume than Kanred. In this year the "severe" method of dough mixing was not used in the baking test. In other years, the "severe" method, and high speed dough mixer were used, Kanmarq was able to withstand the severe treatment better than Kanred.

The plants used in the freezing trials were grown in the Agronomy greenhouse. Approximately 1500 four-inch clay pots were used in the two years. These pots were filled with a mixture of one part well-rotted manure, one part sand, and three parts of black loam soil.

One seed was planted in each pot and the plants were approximately three months old when exposed to the low temperatures. The pots were placed on benches thirty inches from the ground. Water was applied to the plants each morning in sufficient amounts to keep the plants in a vigorous condition. Greenhouse temperatures were kept within a range of from 50° to 65° F.

The artificial freezing was done in a direct expansion, thermostatically controlled, carbon dioxide machine. Dimensions of the freezing chamber were approximately ten feet long, four feet wide and three feet deep. The

cooling was effected by means of nine coils of pipe surrounding the sides, end, and bottom of the interior of the freezing chamber. The thermostat automatically controlled the temperature within a range of three degrees.

After some preliminary freezing studies made on the parent varieties, it was found that a twelve-hour freezing period with minimum temperatures of about -10° C. caused differential freezing injury. This time and temperature were used in the freezing studies made on the F_3 generation. In freezing the F_4 hybrids and parents, the time was reduced to six hours and the minimum temperature lowered to about -11° C.

The number of pots that were placed in the freezing machine in any one lot ranged from eighty-five to one hundred. The same number of pots from each family was frozen in each lot; i.e., each family was represented equally in each freezing lot. A sufficient number of plants of each parent, Kanred and Kanmarq, were frozen in each lot to act as a check on the hybrid plants frozen in the same lot.

The exact moisture content of the soil when the plants were frozen was not determined, but the plants were watered about six hours before freezing, and the soil was in good tilth. After exposure to low temperatures, the plants

were removed to the greenhouse benches and kept under usual greenhouse conditions. The plants were not hardened before freezing. First notes on freezing injury were taken five or six days after being frozen. A second and final note was taken fifteen to twenty days after freezing. Those plants that survived were grown to maturity and the various plant characters, such as date of heading, awn type, number of culms, number of heads, height, etc., were noted.

A planting of the same hybrid families grown in the greenhouse was made each year in the crop improvement nursery at Manhattan, Kansas, in space-planted eight-foot rows. These plantings made it possible to secure notes on winter survival and agronomic characters under field conditions.

Throughout this paper the term "family number" refers to the numbers assigned to the original thirteen F_2 cultures that were grown at Davis, California. Each of these F_2 cultures came from an individual F_1 plant grown in the greenhouse at Manhattan. Most of the data on cold resistance and other characters have been summarized and presented according to these thirteen original pedigrees. The differences found in these progenies produced from the thirteen F_1 plants probably cannot be attributed to

inherent differences among the F_1 plants, since these were probably alike, genetically.

The differences in cold resistance and other characters which were noted in F_3 and F_4 probably have their origin in the dissimilarity of the F_2 plants selected to plant for the F_3 generation. From the progenies of the thirteen F_1 plants, 104 F_2 plants were selected on the basis of grain quality and awn type. Seed of these selected F_2 plants were used to produce the F_3 generation. An analysis of the data on cold resistance and other characters in F_3 and F_4 on the basis of the pedigrees of each of of the 104 F_2 plants might have been a better method of revealing the genetic differences.

This method, however, would have decreased the number of rows and plants in each comparison to such small numbers that the averages would have been of questionable reliability. In all cases where the data are presented in terms of the average for the family, family referring to the original F_1 plant numbers, the averages of the total F_2, F_3, or F_4 population is also given.

This method of summarizing the data on the characters studied in terms of the pedigrees of the thirteen original F_1 plants does not influence the averages calculated on the entire populations.

Whether the character differences among the plants in the thirteen groups arose through segregation in F_2 or F_3, the same cause would affect the genetic character of the F_4 plants in a given group.

Differences in the progonies coming from the thirteen F_1 plants are presumably due to the random selection of distinct genotypes in the F_2 generation. The F_3 cultures which were grown did not represent the complete F_2 population; i.e., only those F_2 plants that produced grain of good quality and that were fully bearded or awnless were used in planting the F_3 cultures.

EXPERIMENTAL RESULTS

Studies of the F_2 Generation

The F_2 plants of the F_1 families were grown at Davis, California, in 1926-1927. Notes were taken on these F_2 plants in the fall of 1927 at Manhattan, Kansas. The notes taken on these plants are given in Table V.

The most interesting notes taken on the F_2 plants were those of awn type. The awn classes described were awnless, very short tips, short tips, long tips, intermediate, and fully bearded. The number of plants in each awn class is shown graphically in Figure 1.

TABLE V. SUMMARY OF NOTES TAKEN ON F_2 PLANTS OF KANRED x KANMARQ GROWN AT DAVIS, CALIFORNIA, 1926-1927.

Family number	Number of plants	Number of plants in each awn class						Average number heads per plant	Average plumpness of kernels per cent
		Awnless	Very short tips	Short tips	Long tips	Intermediate awns	Fully bearded		
128	34	5	3	6	3	8	9	5.2	84.9
129	33	7	0	5	4	8	9	6.9	79.4
130	30	4	2	3	7	7	7	7.5	83.0
131	25	5	0	8	3	2	7	8.1	81.8
132	30	6	2	8	2	3	9	8.1	81.7
133	27	6	1	3	3	6	8	8.0	83.5
134	27	1	4	6	4	3	9	8.0	77.4
135	32	4	1	4	9	7	7	8.3	82.3
136	33	4	1	9	2	9	8	8.1	81.5
137	33	4	0	4	8	6	11	8.8	81.7
138	33	13	4	3	3	2	8	8.8	80.3
139	34	11	1	6	2	3	11	8.2	82.9
140	33	6	3	8	3	5	8	8.6	80.8
	TOTALS	76	22	73	53	69	111	AVE. 7.9	81.6

Observed ratio 293 awnless and intermediate : 111 bearded
Calculated (3:1) 303 " " " : 101 "
Deviation 10 ± 5.87

$$\frac{D}{P.E.} = 1.70$$

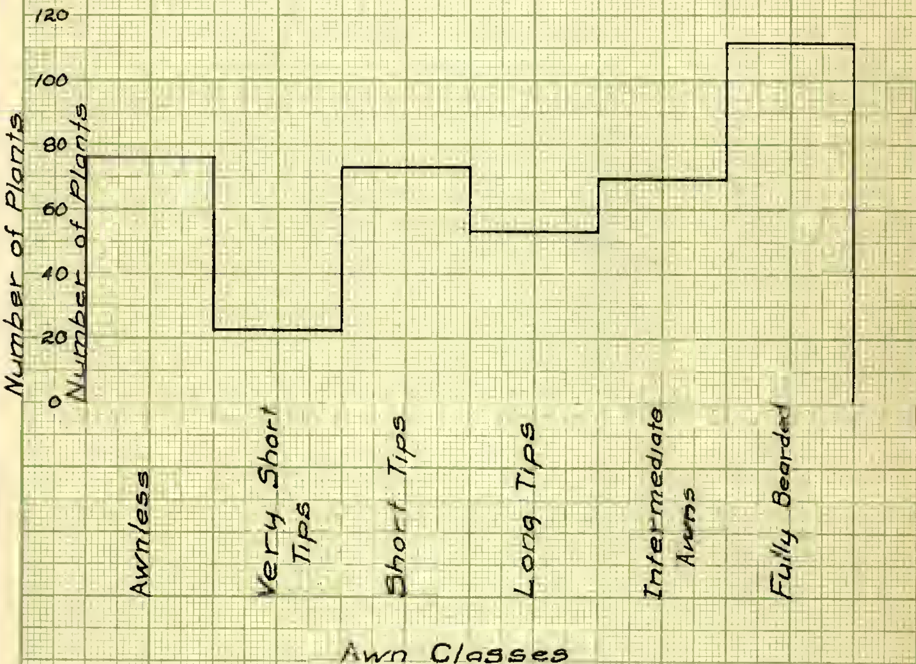

Fig. 1 Distribution of Awn types in F_2 Plants of Kanred x Kanmarq Grown at Davis, Calif. 1926-1927

Clark (5) has used a similar classification in his studies of the inheritance of awn type in wheat. The inheritance of awn type is now recognized as rather complex, and several distinct genotypes are known to be present. If all the plants are placed in two classes, awnless and various intermediates:fully bearded, a ratio of 293:111 is obtained. The fully bearded plants can be determined very accurately, but F_3 tests indicate that mistakes in classifying the other awn types are often made. The expected ratio on factor difference is 303 awnless and intermediate to 101 fully bearded. The deviation from the observed ratio is 10 ± 5.9. Deviations as large as this may be expected to occur through chance sampling, about one-fourth of the time.

From this material the seed was selected for planting eight-foot space-planted rows in the nursery and for a duplicate planting in the greenhouse for artificial freezing studies. Seed for the greenhouse planting was selected from F_2 plants that had a grain plumpness note of 85 per cent or better. No plants of intermediate awn type were selected for planting, only fully bearded and awnless plants were chosen. Seed for the eight-foot space-planted nursery rows was selected from plants with a plumpness note of 80 per cent or better. The following awn types

were represented; awnless, very short tips, short tips, and bearded.

Studies of the F_3 Generation

Greenhouse Experiments. On October 24, 1927, a planting was made which consisted of 1040 plants from the thirteen F_2 families represented. Ten F_3 plants were grown from each F_2 plant selected. Each plant was grown in an individual four-inch clay pot. Two hundred plants of each parent were also grown in individual pots. All of these cultures were placed outside the greenhouse on November 10, or seventeen days after planting. At this time the plants were about three inches tall and had only the primary and secondary leaves. It was thought something might be learned about cold resistance by exposing these plants to outdoor temperatures when they were in the unhardened condition. The pots containing the plants were placed on a level piece of ground near the greenhouse and protected by it on the west and south and by trees on the northeast.

These plants were kept outside from November 10 to December 17, when the hybrids and parents were moved inside the greenhouse and put under greenhouse conditions. Enough water was applied to the plants while they were outside to prevent injury from drouth. A rather severe

cold period December 7 to 10, and 15 to 17, proved fatal to most of the plants. Table VI. gives the maximum and minimum temperatures for the period in which these plants remained outside the greenhouse.

On January 4, 1928, the first notes were taken on the condition of the plants that were subjected to the rather severe conditions outside the greenhouse. Of the 1040 hybrid plants, 626 of these were noted as having a freezing injury of 100 per cent; i.e., as killed. From the 183 Kanred plants, 59 were noted as dead. Sixty-two Kanmarq plants of 174 tested were killed.

Many plants that were not dead at the time the first notes were taken died later. The leaves turned yellow and the plants resembled the injury caused by the lack of plant food. To make sure that this yellowing and dying was not caused by a lack of plant food, a nutrient solution was prepared and applied to the soil in each pot.

This solution was suggested by Doctor M. C. Sewell and consisted of stock solutions containing 236 grams of $Ca(NO_3)_2$ in one liter of water, 136.1 grams of KH_2PO_4 in a liter and 246.3 grams of $MgSO_4$ dissolved in one liter of water. From these stock solutions, 22.7 c.c. of $Ca(NO_3)_2$, 30.1 c.c. of KH_2PO_4 and 8 c.c. of $MgSO_4$ were taken and made up to one liter, and applied to the plants in a

Table VI. Maximum and Minimum Temperatures
Manhattan, Kansas.
November 10, 1927, to December 17, 1927.

	Degrees Fahrenheit	
	Maximum	Minimum
November 10	81	47
11	73	32
12	50	21
13	62	34
14	68	36
15	37	24
16	41	21
17	38	26
18	33	23
19	35	29
20	51	33
21	69	44
22	53	29
23	33	28
24	63	22
25	63	35
26	60	43
27	52	38
28	64	32
29	62	41
30	43	27
December 1	44	16
2	33	9
3	61	23
4	46	17
5	53	19
6	60	36
7	37	3
8	12	-6
9	35	12
10	28	8
11	24	11
12	52	21
13	58	42
14	52	27
15	38	9
16	36	4
17	30	9

quantity that could be held by the pot, which was about one-half pint.

This solution did not seem to benefit the plants to any appreciable extent. The roots of many of these yellowed plants were examined and in most cases were found to be blackened and decayed. Doctor E. C. Miller, of the Department of Botany, suggested that the temperature of the soil in the four-inch pots reached such a low point that the growing root tips were killed. The visible effect on the tops of the plants may have resembled deficient nutrient injury due to the inability of the roots to absorb plant food.

On January 18, 1928, a second and final note was taken on the hybrid and parent plants. Of the 414 hybrid plants not marked dead on the first date, 281 were noted as dead at the time of the second observation. This only left 133 F_3 hybrid plants which survived, out of the original number of 1040. A summary of the number of plants survived from each family is given in Table VII. The same data are presented graphically in Figure 2. The per cent of survived plants of the parental varieties is much greater than of the hybrids.

The survival percentages of the parent varieties are in the order in which they are known to survive under

Table VII. Summary of freezing data on F3 plants of Kanred and Kanmarq and parents frozen outside the greenhouse - Manhattan, 1927

Ped. No.	No. plants grown in each line	No. of plants completely killed	No. of plants that produced grain	Percent of plants that produced grain
128	110	110	0	0
129	140	102	38	17.1
130	60	43	17	28.3
131	100	85	15	15.0
132	80	71	9	11.3
133	90	78	12	13.3
134	50	42	8	16.0
135	80	71	9	11.3
136	80	72	8	10.0
137	90	82	8	8.9
138	40	35	5	12.5
139	80	77	3	3.8
140	40	39	1	2.5
Totals & Ave.	1040	910	133	10.3
Kanred	183	85	98	53.6
Kanmarq	174	97	77	44.3

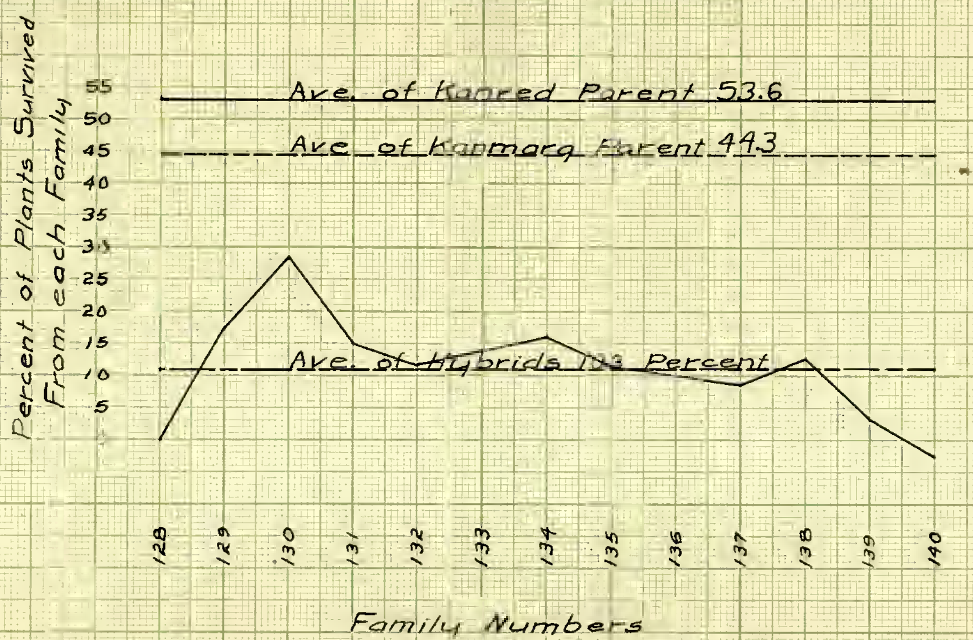

Fig 2 Freezing Results on F_3 Plants of Kanred x Kanmarq Hybrids and Parents Grown in Pots and Frozen outside the Greenhouse Manhattan, Kansas. 1927

field conditions; i.e., Kanred is hardier than Kanmarq. The average difference of about ten per cent is not as great as usually exists between these varieties under field conditions. There are measurable differences in the hardiness of the hybrid families. Family 130 has the highest survival percentage, 28.3, from a total of sixty plants grown. Family 128 is evidently the least hardy, having no survived plants out of 110 plants grown.

The results obtained from this outdoor freezing experiment with young, unhardened plants suggests that cold resistance in this cross may be a recessive character dependent on multiple factors. However, a number of factors, other than the inherent ability of the hybrids and parents to withstand low temperatures, may have influenced the results obtained in this experiment. Observations made during the time these plants were outdoors indicated that those plants that were in pots on the border of the bed were more severely injured than those in the center. This may have been due to the soil in those pots drying out faster, or to less protection from cold by surrounding pots. The planting order was arranged according to families; i.e., family 128 was first in the bed and family 140 was last. These two families were on either end of the bed which may account for their having the lowest

percentages of survived plants.

The results obtained from this outside freezing trial are difficult to interpret due to the fact that such a large per cent of the hybrid plants were killed, only 10.3 per cent survived.

A second planting was made on November 18, 1927, which was an exact duplicate of the planting made on October 24, and frozen in pots outside the greenhouse. This second lot of plants of Kanred x Kanmarq hybrids and parent varieties were grown in the greenhouse until February 13, 1928, before the freezing was started. At that time the plants were seventy-five days old. They were well tillered, prostrate in growth and in a vigorous, healthy condition.

The F_3 families planted represented 104 individual F_2 plants. Each of the thirteen families was represented by from four to fourteen lines of F_3 plants. Each line contained ten plants. The plants of this second planting were numbered from eleven to twenty in order to readily distinguish them from the plants of the first planting, which were numbered from one to ten.

Family 129 is represented by fourteen lines, the largest number. Family 138 and family 140 are represented by only four lines each.

One hundred plants of each parent variety were grown and frozen with the hybrids, to serve as checks or controls.

The method followed in freezing the hybrids was to have each line represented equally in all freezing lots. In order to do this in a consistent manner, plants numbered 11 from all lines were frozen in lot No. 1; plants numbered 12 from all lines were frozen in lot No. 2, and so forth. Plants numbered 20 from each line were not frozen and were used as hybrid checks, to secure data on agronomic characters and to insure a source of seed from each line in case of complete killing of the other plants during freezing. Eight plants of each parent were frozen in every lot, making a total of 72 plants of each parent variety.

The temperatures maintained in the freezing chamber, and the time the plants were put in and taken out of the freezing chamber are shown in Table VIII. Freezing was started on February 13 and completed on February 17, 1928. A twelve-hour freezing period proved to be convenient because plants could be put in and taken out of the freezing chamber in the morning and evening, in this way making efficient use of the freezing machine. Minimum temperatures varied from -10.5° to -9.0° C. Plants in lots 1, 2 and 6 were subjected to the lowest temperatures and as is shown in Table IX., plants of the parents and hybrids were

Table VIII. Record of the Time and Temperature during the Freezing of F_3 Kanred x Kanmarq Hybrids, Agronomy Greenhouse, 1927-1928

Lot no.	Date Feb. 1928	Time put in the freezing chamber	Time taken out of the freezing chamber	Hours frozen	Temperature C. Max.	Min.
1	13	7:30 p.m.	7:30 a.m.	12	-7	-10.5
2	14	7:30 a.m.	7:30 p.m.	12	-7	-10.5
3	14	7:30 p.m.	7:30 a.m.	12	-6.5	- 9.5
4	15	7:30 a.m.	7:30 p.m.	12	-6.5	- 9.5
5	15	7:30 p.m.	7:30 a.m.	12	-6.5	- 9.5
6	16	7:30 a.m.	7:30 p.m.	12	-7	-10.0
7	16	7:30 p.m.	7:30 a.m.	12	-6	- 9
8	17	7:30 a.m.	7:30 p.m.	12	-6	- 9
9	17	7:30 p.m.	7:30 a.m.	12	-6	- 9

Table IX. Relative freezing injury of F_3 plants of Kanred x Kanmarq and parents grown in the Agronomy Greenhouse, Manhattan, Kansas, 1927-1928

Lot no.	Date frozen Feb. 1928	Kanred		Kanmarq		F_3 Hybrids	
		No. of plants	Per cent injury	No. of plants	Per cent injury	No. of plants	Per cent injury
1	13	8	83.8	7	80.6	90	80.4
2	14	8	100.0	8	100.0	79	94.3
3	14	8	36.2	8	79.4	92	23.8
4	15	8	82.5	8	100.0	84	64.1
5	15	8	25.0	8	41.2	90	10.8
6	16	8	76.2	8	81.9	87	76.3
7	16	7	51.4	8	64.4	86	31.9
8	17	8	76.9	8	72.5	81	50.4
9	17	8	36.2	8	30.0	72	17.5
Total numbers and averages		71	63.1	71	72.2	761	49.9

injured the most in these three lots. Lots 7, 8 and 9 received less severe freezing treatments and in these three lots the hybrid plants and parents were less severely injured. The minimum temperatures were kept within a range of 1.5° C. Even with this narrow range, the lower temperatures caused such severe injury that the desired differential results could not be obtained due to complete killing of many plants. The upper limit of this range was not severe enough to cause injury to many plants. These data illustrate the sensitiveness of young, unhardened wheat plants to low temperatures and the difficulties of obtaining differential killing of the plants.

Notes on relative freezing injury of lots, as recorded on the plants nine days after they were frozen, are summarized in Table IX. It seems clear that the uniform temperatures maintained during the freezing of these plants would not account for the variations obtained in the various lots frozen. One of the outstanding differences noted early in the course of the freezing experiment was that of different injury to plants frozen during the day and at night. The parent varieties and the hybrids were both more severely injured when frozen in the daytime. The freezing injury to plants varies according to the

twelve-hour period used; i.e. day or night freezing, as shown in Figure 3. It is clearly evident that lots 2, 4, 6 and 8 frozen in the daytime are more severely injured than the lots with numbers which were frozen at night. The differences in day and night freezing for the parent varieties and for the hybrids are shown in Table X. and Figure 4. Plants frozen in the daytime with temperatures the same as used at night were injured about twice as much as plants frozen at night.

A possible explanation of this difference in day and night freezing results is that plants frozen in the daytime, which have been in the dark during the previous twelve hours, have used up their surplus carbohydrates and sugars that were manufactured during the day, and therefore the concentration of the cell sap is low. On the other hand, plants frozen at night, and found to be more hardy, may have a higher concentration of cell sap, built up during the preceding twelve hours of daylight when carbohydrates were manufactured by the process of photosynthesis.

This hypothesis is supported by the studies of Martin (13), although in these experiments similar material was used, instead of a series of varieties differing in cell sap concentration. Differences in cell sap concentration

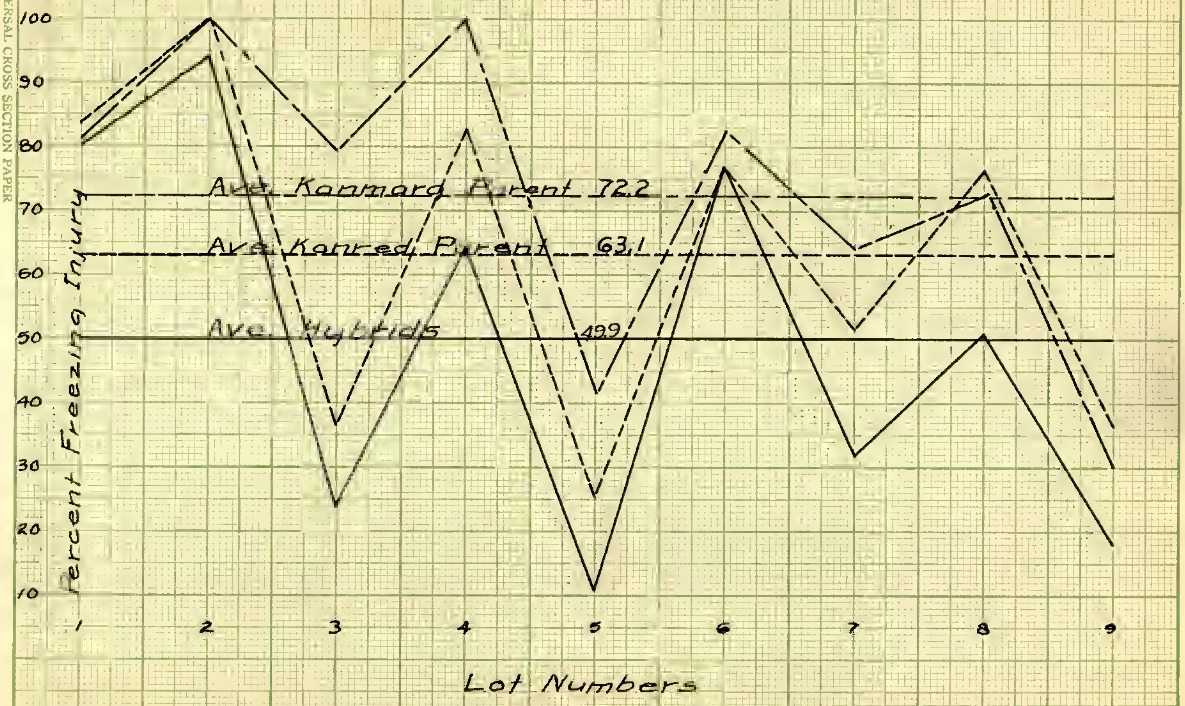

Fig. 3 Relative Freezing Injury of F_3 Plants and Parents of Kanred x Kanmarq Grown in Greenhouse 1927-1928.

Table X. Comparative injury to plants of Kanred, Kanmarq and their F_3 hybrids frozen during the day and night. Agronomy Greenhouse, Manhattan, Kansas, 1927-1928

Plants frozen in the daytime			Plants frozen at night		
Lot no.	No. of plants	Average per cent freezing injury	Lot no.	No. of plants	Average per cent freezing injury
KANRED					
2	8	100.0	1	8	83.8
4	8	82.5	3	8	36.2
6	8	76.2	5	8	25.0
8	8	76.9	7	7	51.4
			9	8	36.2
Total and average	32	83.9		39	46.5
KANMARQ					
2	8	100.0	1	7	80.6
4	8	100.0	3	8	79.4
6	8	81.9	5	8	41.2
8	8	72.5	7	8	64.4
			9	8	30.0
Total and average	32	91.1		39	59.1
F_3 HYBRIDS					
2	79	94.3	1	90	80.4
4	84	64.1	3	92	23.8
6	87	76.3	5	90	10.8
8	81	50.4	7	86	31.9
			9	72	17.5
Total and average	331	71.2		430	32.9

Fig. 4 Comparative Injury to Plants of Kanred, Kanmarq, and their F_3 Hybrids, Frozen during the Day and Night Agronomy Greenhouse, Manhattan, Kansas, 1927-1928.

of the material in this study are due to conditions under which the plants were kept in the twelve-hour period just preceding the exposure to low temperatures.

This clear-cut difference in freezing injury caused by freezing the plants during the day and at night would suggest that artificial freezing studies with small numbers of plants frozen at random intervals may lead one to wrong conclusions as to cold resistant sorts, unless due allowance is made for differences caused by environmental conditions. Whether this difference in injury to plants frozen during the day and at night would be observed with hardened material is an open question.

In analyzing the results of the freezing data on F_3 hybrids of Kanred x Kanmarq, the average per cent freezing injury was determined on the progenies of each of the thirteen original families. As mentioned above, each F_2 family was represented by from fourteen to four lines in F_3; i.e., by 40 to 140 F_3 plants.

Table XI., gives the frequency distribution of freezing injury percentages to the plants for F_3 lines of each family, and the average freezing injury for each F_2 pedigree. The 72 plants of each of the parent varieties varied in degree of freezing injury according to freezing lots. Each variety was represented equally in each freez-

Table XI . Relative freezing injury of F_3 lines from F_2 families of Kanred x Kanmarq hybrids grown in the Agronomy Greenhouse, Manhattan, Kansas, 1927-1928

F_2 Ped. number	No. of F_3 lines frozen	Per cent freezing injury 25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	Average freezing injury per cent
128	11			1		1	5	1		1		1	1					48.2
129	14					1	1	3	3	3	1	2						61.2
130	6				1	1	2	1	1									50.3
131	10			1	2	4	1		1		1							47.1
132	8		1		3	1	1		2									46.0
133	9				1	2	1	3	1	1								52.3
134	5		1	2		1	1											40.3
135	7		2	1	1	2	1											38.4
136	8		1	2	1	2	1	1										41.0
137	9			1	5	1	2											42.2
138	4	1		1		1	1											37.9
139	8						3	2	3									56.0
140	4							2		1	1							62.0
TOTAL	104																AVERAGE	49.9
	No. of lots frozen																	
Kanred	9	1		2			1					2		2			1	63.1
Kanmarq	9		1		1					1		1	3				2	72.2

ing lot so that the results for the two varieties are directly comparable.

The hybrid plants had an average freezing injury of 49.9 per cent, Kanred 63.1 per cent, and Kanmarq 72.2 per cent. The hybrid plants on the average were more cold resistant than Kanred, the more hardy parent. The relative cold resistance of Kanred and Kanmarq is in accord with field observations. There is quite a marked variation in the average injury to plants of the thirteen F_2 pedigrees represented in these F_3 cultures. Plants from family 138 were the least injured, 37.9 per cent. Plants in families 129 and 140 were the most severely injured, 61.2 and 62.0 per cent, respectively. In Figure 5, the data on the average freezing injury for each family are presented graphically. The average freezing injury of the hybrids is distinctly below that of the parental varieties.

A frequency distribution of percentages of freezing injury to individual F_3 plants is given in Table XII. A large per cent of the plants were either only slightly injured or were severely injured or killed. This is also true of the plants of the parental varieties. The frequency curve for the hybrids and parent plants is given in Figure 6. Due to the fact that the plants were either severely injured or only slightly injured, a "U" curve was

Table XII. Distribution of freezing injury percentages of individual F_3 plants of Kanred x Kanmarq, and parents, grown in the Agronomy Greenhouse, Manhattan, Kansas, 1927-1928

	Percent freezing injury											Total no. of plants frozen	Average
	0-5	10-15	20-25	30-35	40-45	50-55	60-65	70-75	80-85	90-95	98-100		
Kanred	6	3	4	6	4	4	7	4	6	8	19	71	63.1
Kanmarq	3	1	3	6	4	3	2	11	4	12	22	71	72.2
F_3 hybrids	112	88	52	51	51	44	61	72	65	67	98	761	49.9

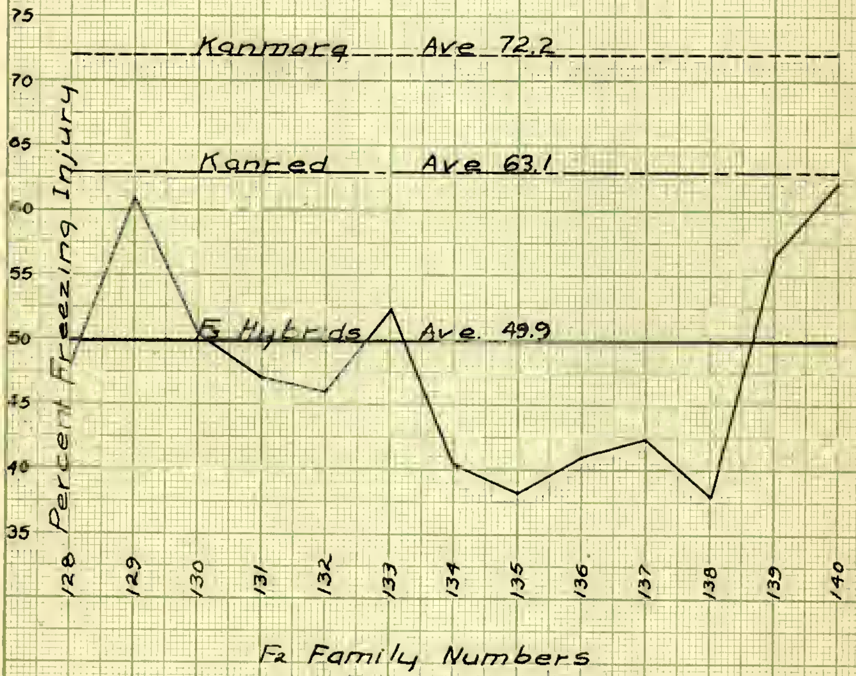

Fig. 5 Relative Freezing Injury of F_3 Lines from F_2 Families of Kanred x Kanmarq and Parents, Grown in the Agronomy Greenhouse. 1927-1928.

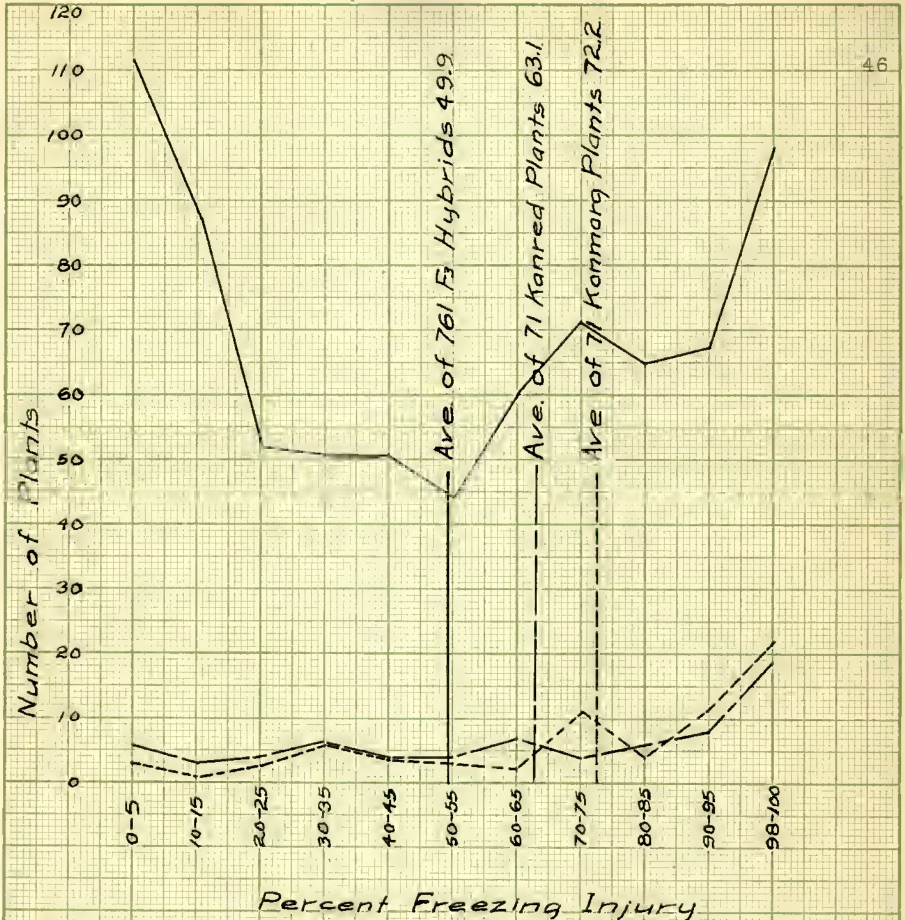

Fig. 6 Distribution of Freezing Injury Percentages on Individual F_3 Plants of Kanred x Kanmarq and Parents, Grown in the Agronomy Greenhouse. 1927-1928.

obtained. The fact that day and night freezing gave widely different results was an important factor influencing the type of curve. Plants frozen at night were only moderately injured while plants frozen in the daytime were severely injured, even though about the same temperatures were maintained.

It was observed during the heading of the F_3 hybrids that plants which had been frozen were delayed in heading, compared to the unfrozen plants in the same pedigrees used as checks. The average heading dates of lines in each of the thirteen families are given in Table XIII. The averages were determined separately on the frozen and unfrozen plants. Differences of five to fifteen days were found to exist between the average heading dates of frozen and unfrozen plants of the same families. The average heading date of 103 unfrozen hybrid plants was April 28 and the heading date of 241 frozen plants was May 8. This is a difference of eleven days. The difference in the heading dates of frozen and unfrozen plsnts of the parental sorts was even greater. Kanred had a difference of seventeen days, and Karmarq a difference of fourteen days, between the average heading dates of frozen and unfrozen plants.

A study was made of the awnless and bearded types and of the relation of these types to certain other

Table XIII. Heading dates of fozen and unfrozen F_3 plants of Kanred x Kanmarq and parents grown in the Agronomy Greenhouse, Manhattan, Kansas, 1927-1928

F_2 Ped. number	No. of F_3 plants from each F_2 family: Unfrozen	Frozen	Dates headed: Unfrozen plants	Frozen plants
128	11	18	Apr. 29	May 9
129	14	38	30	12
130	6	13	24	7
131	10	21	25	6
132	8	21	24	7
133	9	17	27	12
134	5	13	28	7
135	7	20	30	8
136	8	15	27	9
137	9	24	28	10
138	4	14	May 3	8
139	8	22	Apr. 27	7
140	4	5	26	5
Totals and averages	103	241	Apr. 27	May 8
Kanred	29	24	Apr. 28	May 14
Kanmarq	28	24	Apr. 28	May 11

characters. These data are given in Table XIV.

Table XIV. Comparison of agronomic characters of awnless and bearded segregates of F_3 plants of Kanred x Kanmarq, grown in Agronomy Greenhouse, Manhattan, Kansas, 1927-1928

	No. of plants	Average no. of culms per plant	Average no. of heads per plant	Average height of plants inches	Average plumpness of kernels per cent
Awnless	126	5.2	4.7	20.8	82.2
Bearded	220	4.8	4.7	19.9	85.4
Kanmarq	50	4.4	4.0	19.0	87.0
Kanred	52	4.5	4.1	18.6	88.6

Awnless and bearded plants of this cross do not differ greatly in plant height. The awnless plants are about one inch taller than the bearded plants. This difference is in the same order as the awnless and bearded parents; i.e., Kanmarq is a little taller than Kanred. The awnless plants produced more culms per plant, but the number of heads produced per plant by each type was the same. The average plumpness per cent of the kernels of the bearded types was 3.2 per cent higher than the plumpness of the grain produced by the awnless types. This difference in the kernel plumpness of bearded and awnless types is in accord

with the usual qualities of awnless and bearded wheats under semi-arid conditions. Under these conditions, bearded wheats usually produce plump grain of better quality than awnless wheats.

Nursery Experiments. The F_2 plants selected for planting in nursery rows were chosen on the basis of plumpness of grain and awn type. Only those plants that had grain plumpness of 80 per cent or more, and that were classified as awnless, very short tips, short tips or bearded were planted. The thirteen F_2 families or progenies from individual F_1 plants were represented by from twelve to twenty-one rows each. Two hundred and one rows made up the F_3 population grown in the nursery during the season of 1927-1928. Kanred and Kanmarq checks were planted alternately every twenty-fifth row. This planting order only provided four rows of each parent variety, a smaller number of parental checks than is desirable. Seeds were space-planted, three to four inches apart in the rows. The total number of plants per row, determined by counting in the fall, varied from sixteen to twenty-four. Another count was made in the spring, so that the percentage of winter survival for each row could be determined.

Before harvest the promising rows were marked and from these promising rows individual plants were harvested.

Only the most desirable plants from each row were harvested individually, and the remaindor of the plants of each row were harvested and threshed in bulk. Notes were taken on these bulk samples of grain. The seed used in planting tho F_4 population was always from individual F_3 plants. The bulk samplos of grain were used only for quality studies.

During harvest of the individual F_3 hybrid plants and parent variotles, notes wero taken on the number of culms and the number of heads produced. After threshing, the weight of grain for each plant was determined and tho plumpness of the grain of each plant was noted. The total grain yield of each row was calculated by adding the grain weights of tho individual plants, and the weight of the grain produced by tho bulked plants.

Significant differences in winterhardiness occur among the thirteen families. The range of survival among individual F_3 lines was wide, extending from the non-hardy class, 0-49 per cent, to the hardy class, 95-100 per cent. The survival percentages of the thirteen families range from 92.2 por cent for family 138 to 74.9 per cent survival for family 131. It is interesting to noto that family 138 also showed the least freezing injury in the greenhouse freezing experiment

A frequency distribution showing the per cent winter survival of each row in the thirteen families and the average survival for each family is given in Table XV. In no case does the average survival for a hybrid family go beyond the range set by the parent varieties. Kanred had an average winter survival of 93.1 per cent. The corresponding figure for Kanmarq was 72.2 per cent. These averages are only based on four rows of each parent variety and therefore cannot be regarded as very reliable, although they are in agreement with other data on winter survival of these varieties. The average survival of 201 F_3 hybrid rows is 85.8 per cent.

The average percentages of winter survival of each of the thirteen hybrid families and of the parent varieties are shown graphically in Figure 7. It is clearly illustrated by this graphical presentation that the F_3 hybrids are intermediate between the parents, in winter survival; i.e., the hybrids, on the average, are more hardy than Kanmarq and less hardy than Kanred.

The distribution of the rows of the F_3 population for per cent winter survival is given in Figure 8. A normal curve was not obtained. Th curve is skewed with the greater per cent of rows with high percentages of winter survival. Four rows had a survival per cent of less than

Table XV. Winter Survival of F3 families of Kanred X Kanmarq grown in the Agronomy Nursery, 1927 - 1928.

F2 Ped. No.	No. of F3 rows from each F2 family	0-49.9	50.0-54.9	55-59.9	60-64.9	65-69.9	70-74.9	75-79.9	80-84.9	85-89.9	90-94.9	95-100	Av
						Percent Survival							
128	21	1		1	2	1	3	4	2	2	3	2	76.8
129	18				1			1	3	7	3	3	87.4
130	12					1	1	1	3	3	3		83.8
131	14	1	1	1		3	1	1	2	3	1	1	74.9
132	18			1				2	5	5	1	3	84.8
133	12					1		4	3		4		82.2
134	13		1			1	1	1		6	3		80.8
135	12							2	1	2	5	2	89.4
136	13	1	1	1	1	1	1		3	2	1	1	75.3
137	13	1		1		1	1		4	1	2	2	80.6
138	19								1	6	4	8	92.2
139	19					1			4	4	5	5	87.7
140	17						3	1	3	1	5	4	89.9
Total number	201	4	3	5	4	10	11	17	34	42	45	31	83.8
Kanred	4								1		2	1	93.1
Kanmarq	4				1	1		1	1				72.2

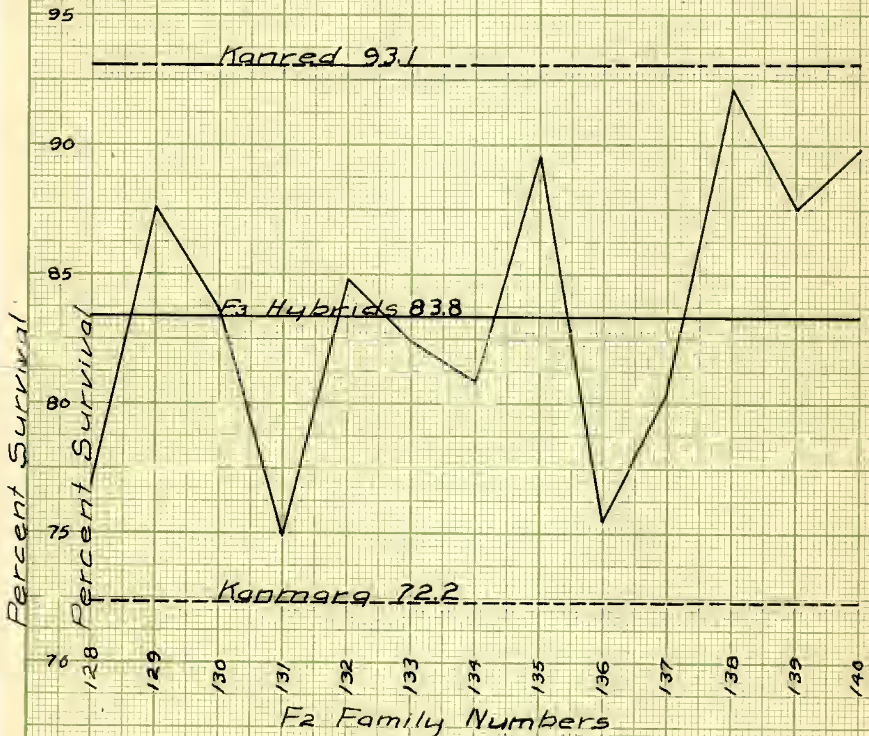

Fig. 7 Winter Survival of F_3 Families of Kanred x Kanmarq, Grown in the Agronomy Nursery, Manhattan, Kansas, 1927-1928.

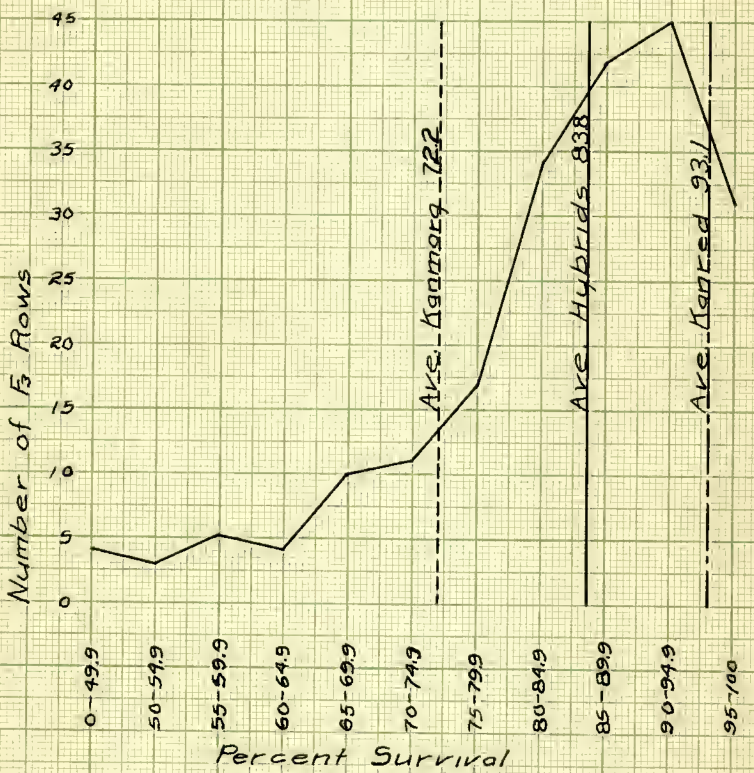

Fig. 8 Winter Survival of F_3 Families of Kanred x Kanmarq, Grown in the Agronomy Nursery, 1927-1928.

fifty. The mode of the curve is in the 90 to 94.9 per cent survival class. Thirty-one rows, or over ten per cent of the total number of hybrid rows, showed complete survival; i.e., no plants winterkilled. The type of curve obtained is certainly influenced by the severity of the winter in which the hybrids were grown. A winter with more severe conditions might have caused a radical change in the type of curve; i.e., the mode might have been at the low survival side with only a few rows surviving 90 to 100 per cent.

In order to see whether there was any relation between the winter survival of awnless and bearded types, the per cent survival of each of these types was determined. There is no significant difference between the winter survival of awnless and bearded rows as shown in Table XVI.

Table XVI. Winter survival of awnless, segregating and bearded F_3 cultures of Kanred x Kanmarq grown in Agronomy Nursery, Manhattan, Kansas, 1927-1928

Awn type	No. of F_3 rows	Average winter survival per cent
Awnless	77	83.8
Segregating	26	88.9
Bearded	96	82.9
Kanred (bearded)	4	93.1
Kanmarq (awnless)	4	72.2

For some reason the segregating rows are somewhat higher in survival, tho percentage being 88.9 as compared with 83.8 and 82.9 for the awnless and bearded types, respectively. The number of segregating rows is considerably less than the other two awn classes which may explain in part the difference in survival. Probably the difference is influenced by chance location and other variations of environmental conditions.

The yields of grain per row in grams were averaged separately for each awn type. Summarized data on yields according to awn type are presented in Table XVII.

Table XVII. Yields of awnless and bearded F_3 type of Kanred x Kanmarq grown in the Agronomy Nursery, Manhattan, Kansas, 1927-1928

	No. of rows	Average yield, grams per 8-foot row
Awnless types	45	193.2 ± 5.160
Bearded types	52	216.4 ± 4.338
Difference		23.2 ± 6.741 $P.E._{diff.}$

The average yields of the awnless and bearded types, based on the yields of 44 and 52 rows, respectively, should be reliable. The average yield of the awnless rows is

193.2 grams, and of the bearded rows, 216.4 grams. This is a difference of 23.2 ± 6.74 grams in favor of the bearded rows. In nine of the thirteen families grown, the bearded progenies outyielded the awnless ones. In only three cases did the awnless types outyield the bearded. In one case, family 139, the awnless and bearded types yielded the same. The thirteen segregating rows yielded an average of 223.9 grams per row. This high yield of the rows segregating for awn type may be correlated with their higher average winter survival. Kanred yielded 231.7 grams and Kanmarq only 98.8 grams per row. The small number of parental check rows and the rather small number of rows segregating for awn type make these yield comparisons of questionable value.

The yields of awnless and bearded rows for each of the thirteen families are shown graphically in Figure 9. As is illustrated in the graph, family 136 is the lowest yielding, and family 140 is the highest yielding.

In order to study the relation between yield of grain per row and the per cent winter survival, a correlation was calculated for these two characters. The value of "r", the correlation coefficient, was .163 ± .063. This low value suggests that no significent correlation existed

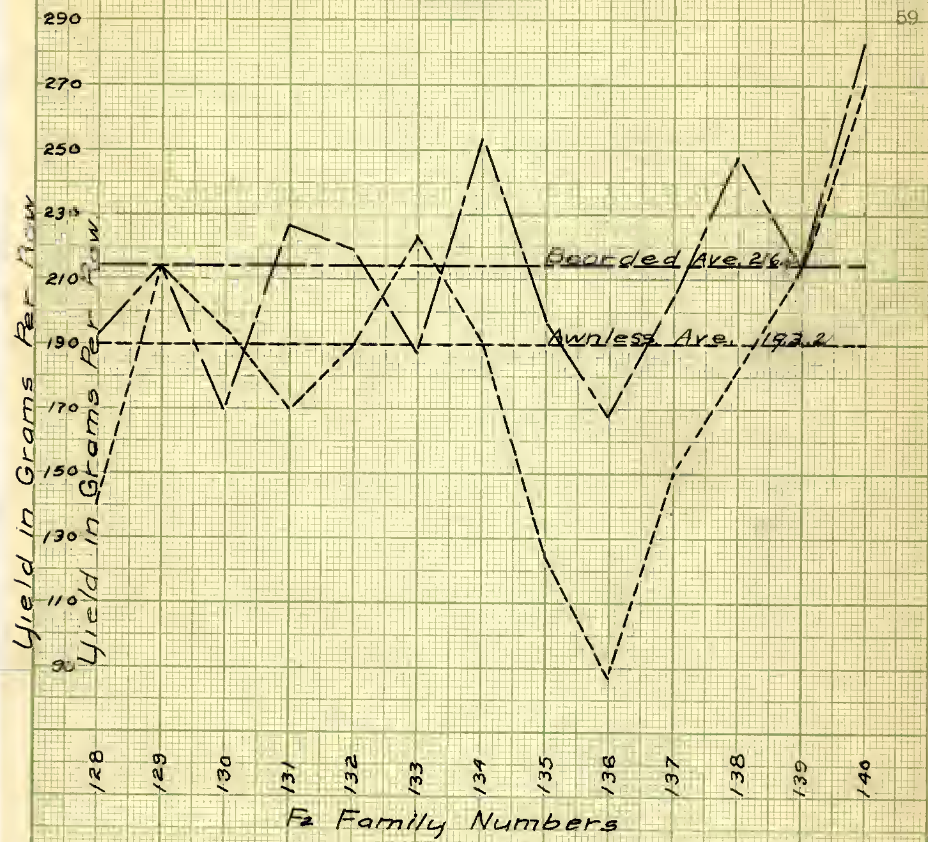

Fig. 9 Yields of Awnless and Bearded F_3 Types of Kanred x Kanmarq Grown in the Agronomy Nursery, Manhattan, Kansas, 1927-1928.

between yield and per cent of winter survival under the methods used in handling these F_3 hybrid rows. A probable explanation for this lack of correlation between winter survival and yield lies in the fact that only those rows that survived 80 per cent or better were harvested. Thus the rows on which yield was determined, all had rather high winter survival.

It is probable that if all rows had been harvested, those with low winter survival percentages would also have had low yields, thus giving a higher value of the corelation coefficient. The conclusion to be drawn from these data is that rows that survive 80 per cent or better have enough plants to make efficient use of the available ground and are able to yield about as much as rows containing perfect stands; i.e., with 100 per cent survival.

The distribution of plumpness percentages of grain from rows of each family and the average plumpness of the grain for each family are shown in Table XVIII. The average kernel plumpness of the different families does not vary widely. The hybrids produced grain of about the same plumpness as the parent varieties. Kernels of Kanred were somewhat more plump than those of Kanmarq.

The weight of grain and the kernel plumpness were determined for each of the individual plants harvested.

Table XVIII. Distribution of kernel plumpness percentages of F_3 plants of Kanred x Kanmarq, and parents, Agronomy Nursery, Manhattan, Kansas, 1927-1928

Ped. no.	No. of F_3 rows	Kernel plumpness, per cent 78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	Average
128	7								2	1							1	2		1		90.4
129	13													3		2	1	3	3		1	93.2
130	7												2	1	2	1		1				90.9
131	4					1						1					1		1			89.5
132	11													2	2	1	3	1	1	1		92.5
133	6														1				1	4		95.0
134	6													1	2			2	1			92.5
135	8						1				1	2	1	1	1	1						88.5
136	2								1					1								87.5
137	9									1	2	1	1	1	2	1						88.8
138	17	1		1					1	1	2			5	3	1	1	1				88.5
139	12												1	1	3	2	1	3	1			92.1
140	3																	1	2			94.7
Total and average	105	1	0	1	0	1	1	0	4	3	5	4	5	16	16	9	8	14	10	6	1	91.0
Kanred															2		1	1				92.3
Kanmarq											1	1			1	1						89.5

The correlation between the average weight of grain per plant and the plumpness of kernels was determined. The value of "r" was found to be .372 ± .0563 which is statistically significent but is not a high value. The plants that produced the plumpest kernels also showed a tendency to produce the most grain.

The date of first heading was recorded on 196 F_3 hybrid rows grown in the nursery. In order to distinguish any significant differences in families, the heading dates on rows of each family were averaged separately. Table XIX. shows the distribution of heading dates for rows in each family. There is a fairly wide range between the first and last rows to head in most of the thirteen families. With such a wide range the average heading date for the family does not give a complete picture of the true nature of each line. The range in heading dates within each of the thirteen families varied from six to eleven days. The average heading date of all F_3 hybrid rows was May 23, intermediate between the parent varieties.

Family 128 has the latest average heading date, May 26, and families 139 and 140 are the earliest, heading on May 21. The average heading dates of the parents are based on the average of only four rows each, and therefore are of doubtful reliability. The distribution of heading

Table XIX. Distribution of the heading dates of Kanred, Kanmarq, and their F_3 hybrids grown in the Agronomy Nursery, Manhattan, Kansas, 1927-1928

Ped. no.	No. of F_3 rows	Heading dates MAY 18	19	20	21	22	23	24	25	26	27	28	29	30	Range	Average MAY
128	21				1		2	2	1	8	5		1	1	10	25.8
129	18				1	2	4	6	1	3		1			8	24.0
130	12			1	1	2	1	4		2	1				8	23.6
131	14		1			2	5	3		2	1				9	23.5
132	17	3		2	3	2	1	3		2	1				10	22.0
133	12					1	5	4		1	1				6	23.8
134	13	1	1		2	2	4		2	1					9	22.4
135	12	2		3			3	2		1		1			11	22.3
136	11						2	1		5	1	2			6	25.7
137	11					1	2	3		4		1			7	24.7
138	19				1		5	3	2	8					6	24.5
139	19	2	3	1		7	4	1		1					9	21.5
140	17	2		3	2	4	5	1							7	21.5
Totals and average	196	10	5	10	11	23	43	33	6	38	10	5	1	1	13	23.5
Kanred							1			2	1					25.5
Kanmarq							1	1	2							24.3

dates of all F_3 rows is shown graphically in Figure 10. The curve appears bi-modal in nature, but this type probably is due, in part at least, to the fact that heading notes were not taken every day during the heading period. It is possible, however, that these F_3 rows are really divided into two main groups, genetically, with the early types heading from May 18 to 23, and the late types, from May 26 to 30.

Studies of the F_4 Generation

Greenhouse Experiments. Selections of the Kanred x Kanmarq hybrids were grown and studied in the F_4 generation, along similar lines as in the F_3 generation. Three separate plantings were made in the fall of 1928. Two plantings were made in the greenhouse and one was made in the Agronomy nursery. This field planting consisted of one hundred fifty-four eight-foot, space-planted rows.

One of the two greenhouse plantings was made from seed of F_3 plants that survived the outdoor freezing test of the F_3 generation previously described. This planting consisted of 460 plants, grown in four-inch clay pots. Eleven of the original thirteen families are represented in these F_4 hybrids. All F_3 plants from families 128 and 140 were killed by exposure to severe outdoor conditions

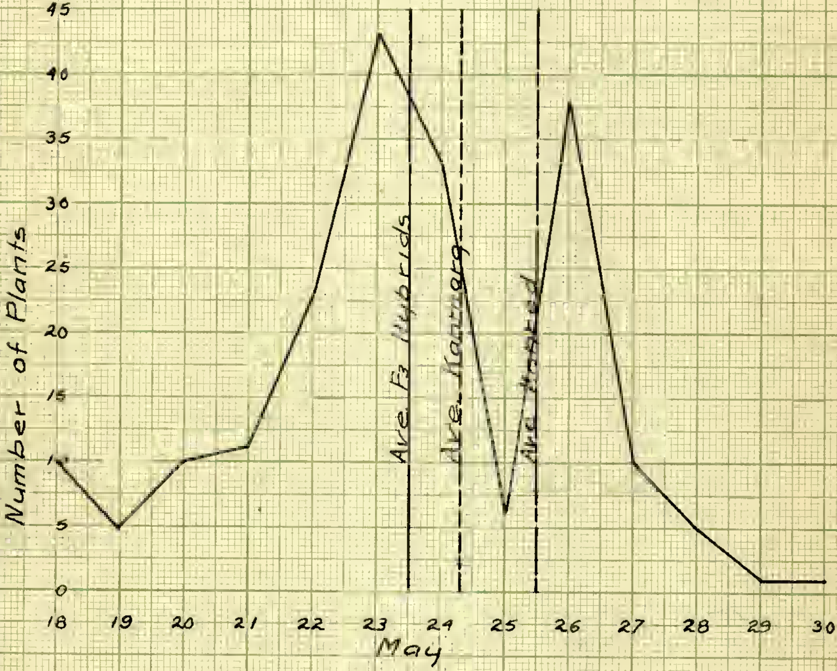

Fig 10 Heading Dates of F3 Rows of Kanred x Kanmarq Hybrids Grown in the Agronomy Nursery, 1927-1928.

and no plantings were possible from these families.

The other F_4 cultures grown in the greenhouse were made from seed of F_3 plants that survived the freezing tests made in the refrigeration machine. This planting consisted of 390 plants, representing all of the original thirteen families. One hundred plants of each parent were grown. These were used as checks in the freezing trials with the hybrid plants. Both plantings were made on October 29, 1928, and kept under the same conditions in the greenhouse. The type of soil, method of watering, etc., were the same as described for the F_3 hybrids. The F_4 material was grown in the same greenhouse and under very similar temperatures and conditions. Those plants that were not frozen, or that survived the freezing test, were grown to maturity in the greenhouse and harvested. One plant from each line was not frozen. These plants provided notes on agronomic characters and insured a source of seed supply in case of complete killing of the plants frozen.

Freezing of the F_4 hybrid plants and parents started on January 8, 1929, and was completed on January 14. The plants were seventy days old when the freezing trials were started. Freezing was divided into thirteen separate lots. Lots 1 to 9 contained the material grown from F_3 plants

that survived the outdoor freezing test. Lots 11 to 14 contained the hybrids grown from F_3 plants that survived the freezing tests made in the refrigeration machine. Lots 10 and 15 were not frozen, but were saved to insure a source of seed. Only five plants were grown from each F_3 plant that survived the indoor freezing test, while ten plants were grown from each F_3 plant that survived the outdoor freezing test.

It was decided that a slight change in the freezing procedure from that used on F_3 hybrids might give better results. This change consisted of using slightly lower temperatures and freezing for a shorter time. It was found, after a few preliminary tests with Kanred and Kanmarq, that a six-hour period with a minimum temperature of about twelve degrees F. gave differential killing of these varieties. The times and temperatures used in freezing each of the lots are shown in Table XX. A six-hour period in the morning and a six-hour period in the afternoon were used. The refrigeration machine was kept running during the night in order to keep the temperature down to the minimum temperature required. During the time that lot No. 9 was being frozen a new supply of CO_2 gas was added to the machine which caused the minimum temperature to be attained soon after the plants were put in the refrigeration chamber. For this reason, the

Table XX. Record of freezing time and temperature of F_4 Kanred x Kanmarq hybrids, Agronomy Greenhouse, Manhattan, Kansas, 1928-1929

Lot no.	Time put in refrigeration chamber	Time taken out refrigeration chamber	Hours frozen	Minimum temperature F.
1	1:00 p.m.	7:00 p.m.	6	13.5
2	8:00 a.m.	2:00	6	13.0
3	2:00 p.m.	8:00	6	11.0
4	8:00 a.m.	2:00	6	11.0
5	2:00 p.m.	8:00	6	11.0
6	8:00 a.m.	2:00	6	12.0
7	2:00 p.m.	8:00	6	15.5
8	8:00 a.m.	2:00	6	14.0
9	2:00 p.m.	8:00	6	12.0
11	8:00 a.m.	2:00	6	12.0
12	2:00 p.m.	8:00	6	12.0
13	8:00 a.m.	2:00	6	12.0
14	2:00 p.m.	8:00	6	12.0

plants in lots 9 to 14 were injured rather severaly.

The percentages of freezing injury for the F_4 hybrids and parents frozen in each lot are given in Table XXI. The average freezing injury of all 710 F_4 hybrid plants was 66.2 per cent. The freezing injury for Kanred and Kanmarq was 77.2 and 84.2 per cent, respectively. These average percentages of freezing injury are in the same order as in the F_3 freezing test. Kanmarq is less cold resistant than Kanred and the hybrids are hardier than Kanred.

The percentages of freezing injury of the hybrids and parents frozen in each lot are shown graphically in Figure 11. There are greater fluctuations in freezing injury of the different lots than would be expected, considering the uniformity of time and temperatures used. The lots frozen in the morning and in the afternoon gave differential results as was the case with the lots of F_3 plants frozen in the daytime and at night.

The differences in freezing injury of the lots frozen in the morning and in the afternoon are clearly shown in Table XXII. and Figure 12. The order of injury for the hybrids and parents is the same in the morning and afternoon lots, but the injury is much greater on plants frozen in the morning. In each case, plants of Kanmarq were more severely injured than plants of Kanred, and in each case the hybrids were more cold resistant than Kanred.

Table XXI. Relative freezing injury of F_4 plants of Kanred x Kanmarq, and parents, grown in the Agronomy Greenhouse, Manhattan, Kansas, 1928-1929

Lot no.	Date frozen JANUARY	KANRED No. of plants	KANRED Per cent freezing injury	KANMARQ No. of plants	KANMARQ Per cent freezing injury	F_4 HYBRIDS No. of plants	F_4 HYBRIDS per cent freezing injury
1	8	3	0.0	5	61.0	45	32.0
2	9	5	91.6	5	99.8	46	86.3
3	9	5	88.8	5	75.0	45	69.5
4	10	5	97.4	5	91.8	43	57.3
5	10	5	12.0	5	60.8	46	49.6
6	11	5	93.6	5	96.4	43	77.7
7	11	5	23.0	5	17.0	46	29.0
8	12	4	95.0	5	99.8	44	86.5
9	12	5	81.0	5	94.6	43	79.8
11	13	5	97.6	5	99.6	77	76.6
12	13	5	92.2	5	99.6	78	57.3
13	14	5	93.8	5	99.6	77	79.9
14	14	5	93.6	5	99.4	77	68.2
Total numbers and averages		62	77.2	65	84.2	710	66.2

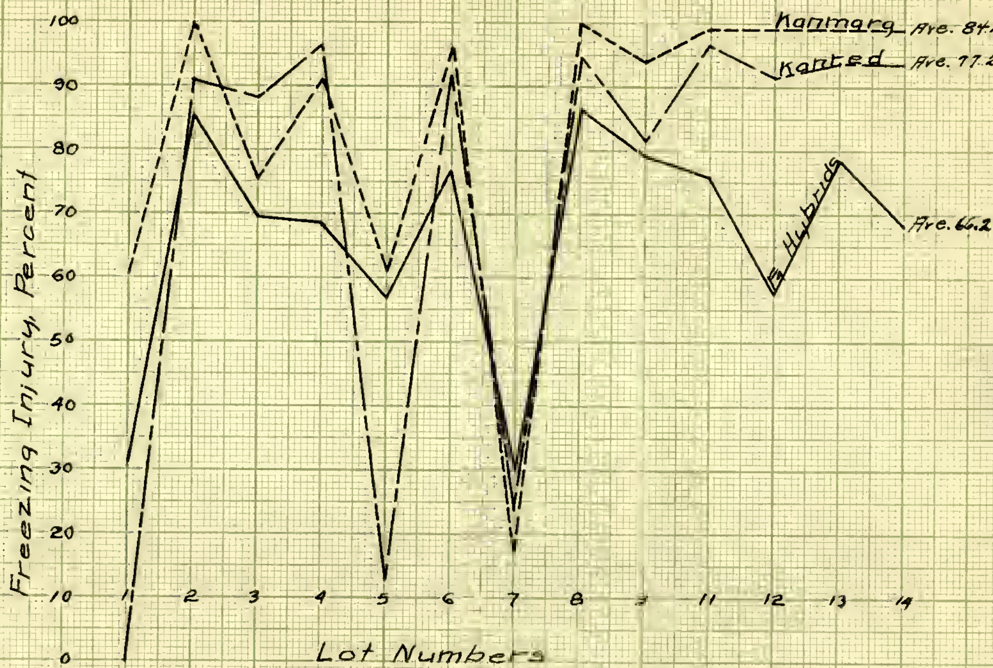

Fig. 11 Relative Freezing Injury of F_4 Plants of Kanred x Kanmarg and Parents, Grown in the Agronomy Greenhouse, 1928-1929.

Table XXII. Comparative injury to plants of Kanred, Kanmarq and their F_4 hybrids, frozen during the morning and afternoon, Agronomy Greenhouse, Manhattan, Kansas, 1928-1929

Plants frozen in the morning			Plants frozen in the afternoon		
Lot no.	No. of plants	Average freezing injury per cent	Lot no.	No. of plants	Average freezing injury per cent
		KANRED			
2	5	91.6	3	5	88.0
4	5	97.4	5	5	12.0
6	5	93.6	7	5	23.0
8	4	95.0	9	5	81.0
11	5	97.6	12	5	92.2
13	5	93.8	14	5	93.6
Total and average	29	94.8		30	65.0
		KANMARQ			
2	5	99.8	1	5	61.0
4	5	91.8	3	5	75.0
6	5	96.4	5	5	60.8
8	5	99.8	7	5	17.0
11	5	99.6	9	5	94.6
13	5	99.6	12	5	99.6
			14	5	99.4
Total and average	30	97.8		35	72.5
		F_4 HYBRIDS			
2	46	86.3	1	45	32.0
4	43	57.3	3	45	69.5
6	43	77.7	5	46	49.6
8	44	86.5	7	46	29.0
11	77	76.6	9	43	79.8
13	77	79.9	12	78	57.3
			14	77	68.2
Total and average	330	77.6		380	56.1

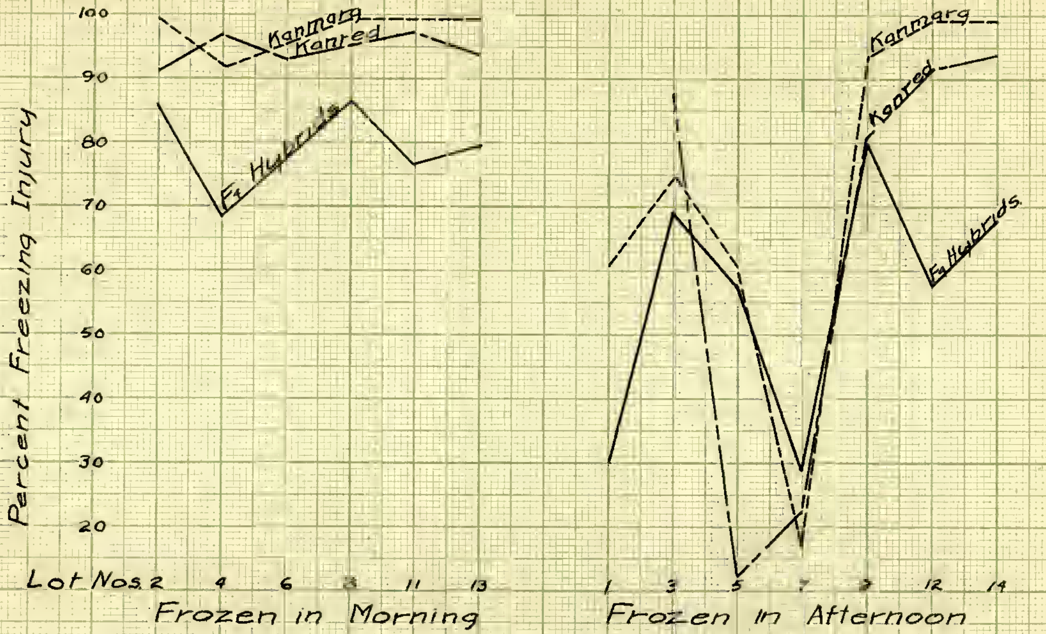

Fig. 12 Comparative Injury to Plants of Kanred, Kanmarg, and their F4 Hybrids, Frozen during the Morning and Afternoon. Agronomy Greenhouse. Manhattan, Kansas. 1928-1929.

The same explanation of this difference in freezing injury of morning and afternoon lots of the F_4 hybrids is suggested as for the F_3 hybrids frozen during the day and at night. Plants frozen in the morning have had a period of twelve hours in the dark during the night and are badly injured. Plants frozen in the afternoon have had a period of six hours daylight preceding the exposure to low temperature and were much less injured. It seems possible that unhardened wheat plants growing in the greenhouse and in a vigorous condition can bring about some changes in their tissues and cell contents within six hours that make them more resistant to cold. Plants frozen after a twelve-hour period of darkness evidently lack the ability to withstand cold. This difference is probably due to a difference in the concentration of the cell sap. This difference in concentration may be due to two causes; first, the transpiration rate is lower in the night, therefore, the plants contain a higher per cent of water, thereby decreasing the concentration and lowering the cold resistance. Second, the sugars and carbohydrates are used in the metabolism of the plant during the night, thus decreasing the concentration of the cell sap. The latter explanation seems the most probable because the transpiration in the greenhouse was probably not sufficient

to bring about an appreciable water loss during the day and to increase the cell sap concentration. In the cereals the carbohydrates are stored in the foliage as sugars. It is known from the work of Akerman (1) that the presence of sugars in the cells of wheat plants has a direct influence on the freezing injury, tending to make the plants more resistant to cold.

Freezing tests on the F_4 hybrids were made separately on the progenies grown from F_3 plants frozen outdoors and on those frozen in the refrigeration machine in the greenhouse. Lots 1 to 9 contained the plants grown from F_3 plants that survived the outdoor freezing, and lots 11 to 14 contained the plants grown from F_3 plants that were frozen in the refrigeration machine. The average percentages of freezing injury for each family in the two lots of material, the average freezing injury of all families in the two lots, and the average injury of all families in both lots are given in Table XXIII.

It was evident that the F_3 plants frozen outdoors received a more severe treatment than the plants frozen in the refrigeration machine. It would therefore be expected that the surviving plants from the outdoor test would produce more hardy progenies in F_4. The data presented in Table XXIII. might be taken as indicating

Table XXIII. Relative freezing injury of F_4 lines of Kanred x Kanmarq grown from F_3 plants which survived in the outdoor and indoor freezing tests of 1927-1928, Agronomy Greenhouse, Manhattan, Kansas, 1928-1929

Ped. no.	Injury to F_4 lines grown from F_3 plants frozen outdoors: No. of F_4 lines	Injury to F_4 lines grown from F_3 plants frozen outdoors: Average freezing injury per cent	Injury to F_4 lines grown from F_3 plants frozen in the greenhouse: No. of F_4 lines	Injury to F_4 lines grown from F_3 plants frozen in the greenhouse: Average freezing injury per cent	General average
128			3	87.9	87.9
129	15	61.7	11	60.2	61.1
130	6	56.6	5	77.8	66.2
131	3	45.0	6	62.6	57.9
132	3	67.6	2	86.0	75.0
133	3	78.3	5	71.0	73.7
134	3	48.0	8	61.0	57.5
135	1	66.7	6	67.5	67.4
136	5	62.7	8	73.7	69.5
137	3	64.3	10	69.7	68.5
138	1	81.6	4	73.9	75.4
139	3	74.2	8	79.0	77.7
140			2	89.8	89.8
Total and averages	46	65.3	78	70.7	68.7
	No. of plants				
Kanred	42	69.1	20	94.3	77.2
Kanmarq	45	77.4	20	99.6	84.2

that this is actually what happened. The F_4 plants grown from F_3 plants frozen outdoors had an average of 65.3 per cent injury, while the F_4 plants grown from F_3 plants frozen in the refrigeration machine showed 70.7 per cent injury. However, in comparing this injury with the per cent freezing injury of the parent varieties which had had no previous differential treatment, it seems evident that the difference in the F_4 hybrids is not due to a genetic difference in cold resistance of the two groups. As was previously mentioned, lots 11 to 14 were more severely injured due to minimum temperatures being reached soon after they were put in the refrigeration machine, which was operating with a fresh tank of CO_2 gas, while these lots were being frozen.

The average freezing injury of all F_4 hybrid lines was 68.7 per cent. The average freezing injury of the parent varieties was 77.2 and 84.2 per cent, for Kanred and Kanmarq, respectively. This order of freezing injury is in accord with the results obtained with the F_3 hybrids. Kanred is more resistant to cold than Kanmarq and the F_4 hybrids are more cold resistant than either parent.

The distribution of percentages of freezing injury on all F_4 hybrid plants and parents is given in Table XXIV. and is shown graphically in Figure 13. The curve obtained

Table XXIV. Distribution of freezing injury percentages, individual F_4 plants of Kanred x Kanmarq and parents, grown in the Agronomy Greenhouse, Manhattan, Kansas, 1928-1929

	Per cent freezing injury											Total no. of plants frozen	Average
	0-9.9	10-19.9	20-29.9	30-39.9	40-49.9	50-59.9	60-69.9	70-79.9	80-89.9	90-97.9	98-100		
Kanred	8	0	3	0	0	0	1	0	9	23	18	62	77.2
Kanmarq	5	2	0	1	0	1	0	1	7	9	39	65	84.2
F_4 hybrids	52	45	42	34	28	26	34	48	124	169	108	710	66.2

Fig. 13 Distribution of Freezing Injury Percentages Individual F_4 Plants of Kanred x Kanmarq and Parents, Grown in the Agronomy Greenhouse, 1928-1929.

in the freezing of the F_4 hybrids is not as distinctly "U" shaped as was obtained in the F_3 generation freezing trials. It more closely resembles a "J" curve. A large majority of the plants are in the classes of severe freezing injury, 80 to 100. More plants of Kanmarq than of Kanred appear in the last two classes, 90 to 100.

A comparison was made of the freezing injury percentages obtained on F_3 plants and their F_4 progenies. The object was to determine the relation between the freezing injury obtained in the two generations. If larger numbers had been available, the correlation method would have been used to determine the relation between freezing injury of F_3 and F_4 families. The average percentages of freezing injury for each family in the third and fourth generations are shown graphically in Figure 14. There is no very consistant relation between freezing injury in the F_3 and F_4 hybrids.

It seems possible to class families 133, 139 and 140 as relatively non-resistant to cold, and families 131, 134, 135 and 138 as relatively resistant to cold. This leaves six families, 128, 129, 130, 132, 136 and 137, that are in question, due to the contradictory results obtained in the two generations.

As was the case during the heading of the F_3 hybrids,

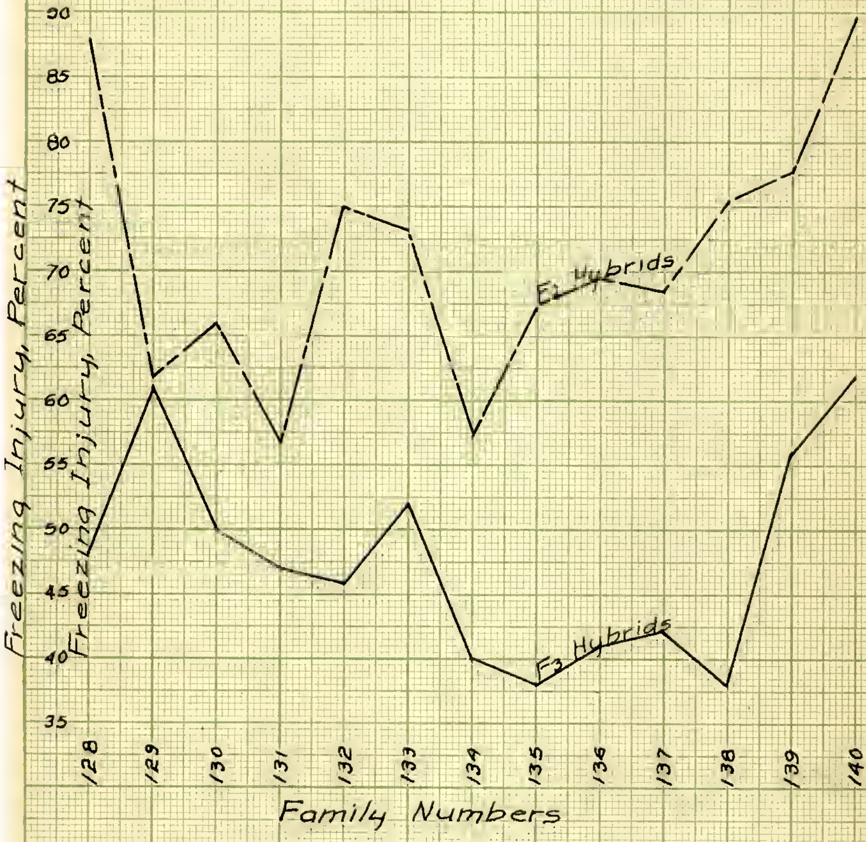

Fig. 14 Relative Freezing Injury to F_3 Lines and their F_4 Progenies. Kanred x Kanmarq. Agronomy Greenhouse. (F_3) 1927-28. (F_4) 1928-29.

it was observed that the F_4 hybrids and parents that were exposed to low temperatures headed later than the unfrozen plants. During the heading of the hybrids and parents each plant was tagged on the date the spike emerged from the sheath, with the date noted on the tag. These dates were recorded at harvest-time. The average heading dates of unfrozen and frozen plants in each family are presented in Table XXV. An average delay in heading of four days was caused by freezing the hybrid plants. Kanred plants, frozen and unfrozen, showed a difference of nine days. Kanmarq plants, frozen and unfrozen, showed a difference of three days.

These results should put investigators on their guard as to studies of heading dates in populations where some of the plants have been injured by freezing, but not killed, and other plants not injured.

Nursery Experiments. One hundred thirty-nine F_4 lines were grown in space-planted eight-foot rows in the Agronomy nursery, at Manhattan, in 1928-1929. The seed planted in each row to produce the F_4 crop was from an individual F_3 plant. These plants were selected on the basis of winter survival, plumpness and quality of grain, yield, and general vigor of the plants. F_3 plants were

Table XXV . Heading dates of frozen and unfrozen F_4 plants of Kanred x Kanmarq and parents, grown in the Agronomy Greenhouse, Manhattan, Kansas, 1928-1929

Ped. no.	Unfrozen: No. of F_4 plants	Unfrozen: Date headed	Frozen: No. of F_4 plants	Frozen: Date headed
128	1	Apr. 29	1	May 12
129	25	May 12	69	18
130	9	11	29	9
131	9	5	28	7
132	5	2	10	3
133	6	12	6	16
134	10	2	27	8
135	7	7	13	10
136	13	5	30	10
137	9	6	25	12
138	4	14	9	16
139	10	7	21	9
140	1	Apr. 27	2	10
Total and averages	110	May 8	270	May 12
	No. of plants			
Kanred	29	May 3	9	May 12
Kanmarq	25	May 10	9	May 13

harvested only from rows showing high survival. This automatically selected only plants from hardy rows for planting the F_4 cultures.

The seed was space-planted, three to four inches apart in the row. Wintersurvival percentages were determined from the plant counts made in the fall and in the spring. This was the same method as used in F_3. One parent variety was planted alternately every tenth row. Only eight Kanred rows and seven Kanmarq rows were grown. These numbers are again too small to provide very reliable data on winter survival and other characters of the parents.

The same general method was used in harvesting the F_4 hybrids as was used in harvesting the F_3 plants. Before harvest the promising rows with a high winter survival were noted and only the desirable individual plants from these rows were harvested. Notes were taken on the plant and grain characters of these individual selections.

A study was made of the per cent winter survival of each of the thirteen original families. The distribution of the survival percentages for rows of each family and the average winter survival of each family are given in Table XXVI. It is clearly evident that the hybrid families differ in the degree of resistance to cold. Family 130 has the highest survival, 95.3 per cent. Family 136 has

Table XXVI. Winter survival of F_4 families of Kanred x Kanmarq and parents grown in the Agronomy Nursery, Manhattan, Kansas, 1928-1929

Ped. no.	No. of F_4 rows	Winter survival, per cent								Average
		60-64.9	65-69.9	70-74.9	75-79.9	80-84.9	85-89.9	90-94.9	95-100	
128	3					1		1	1	91.3
129	13					2	2	3	6	93.5
130	6						2		4	95.3
131	4						2		2	92.8
132	18			1	1	1	1	4	10	93.9
133	5	1				1	1		2	86.2
134	7		1		1	1	1	1	2	86.8
135	15			2	1		2	4	6	90.8
136	3			1			1	1		83.7
137	7			1	1	2	1	1	1	85.2
138	18		1	2	1	2	2	4	6	88.8
139	24				2	3	4		15	93.3
140	16		2		3	3	1	2	5	85.9
Totals and average	139	1	4	7	10	16	20	21	59	90.5
	No. of plants									
Kanred	8				2	2	1		3	88.5
Kanmarq	7			1	1	2	1	2		84.6

the lowest survival, 83.7 per cent. It is of interest to note that in the F_3 generation, family 130 had a relatively high survival and family 136 was the lowest in per cent winter survival. The percentages of winter survival of each F_4 family are shown graphically in Figure 15.

The distribution of F_4 rows according to the percentages of winter survival is shown graphically in Figure 16. The curve is distinctly skewed. The modal point is in the 95 to 100 per cent survival class. The average survival of the F_4 rows is 90.5 per cent, compared with 88.5 for Kanred and 84.6 for Kanmarq. No rows of Kanmarq had survival percentages in the 95-100 class, the modal class for the hybrids.

These data indicate that the F_4 hybrids are more cold resistant than either parent. The selection of F_3 plants from rows surviving 80.0 per cent or better has evidently produced an F_4 generation superior to the F_3 population in hardiness. The F_3 plants as mentioned above were intermediate between the parents in winter survival. The F_4 hybrids consisted of a population selected for cold resistance. The F_3 population was not a selected one, because the F_2 plants were grown at Davis, California, where no winterkilling occurred. Some progress has evidently been made in selecting for cold resistance in the F_3 generation

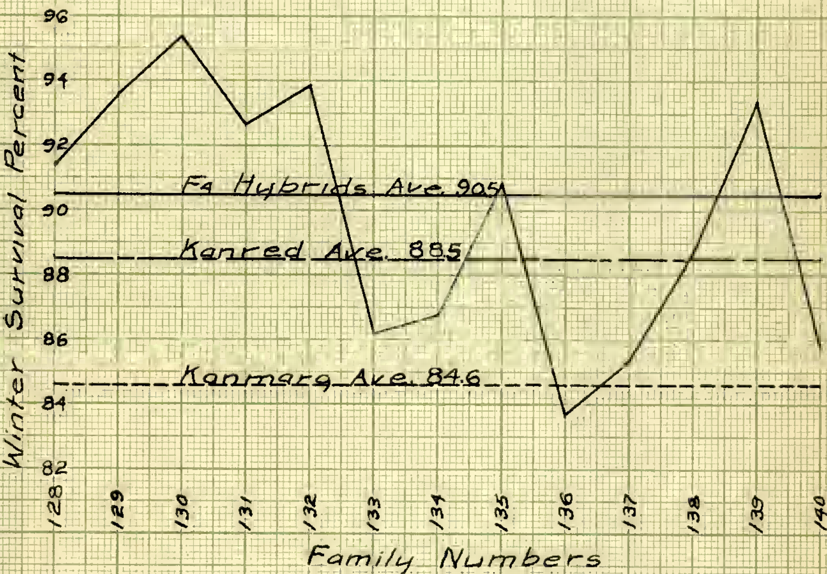

Fig. 15 Winter Survival of F_4 Families of Kanred x Kanmarq Agronomy Nursery. 1928-1929.

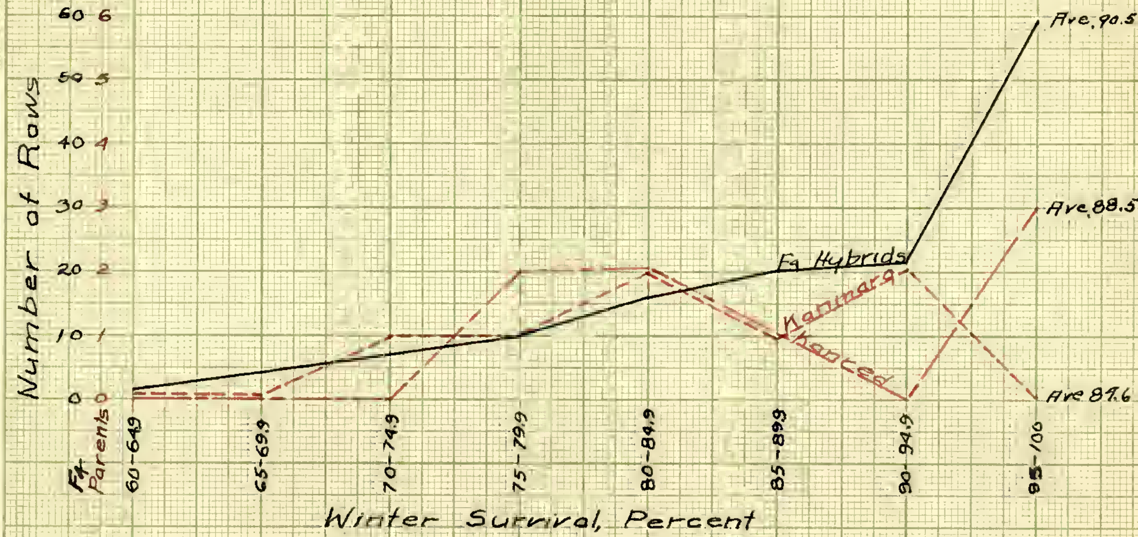

Fig. 16 Winter Survival of F4 Rows of Kanred x Kanmarq, Agronomy Nursery, 1928-1929.

of this backcross. By continued selection in subsequent generations it should be possible to isolate strains that are as hardy as Kanred, or more hardy. Several seasons with conditions favoring differential winterkilling, will be necessary before a strain breeding true for cold resistance can be produced. Many genetic factors determine the cold resistance of wheat plants, and winter survival is also influenced by environmental conditions which cannot be controlled or even accurately measured.

A positive relation was found between winter survival of F_3 hybrids and their F_4 progenies. With such a complex character as winterhardiness, a closer agreement could hardly be expected. Many factors influence the survival of plants, such as chance location, drouth, heaving and injury from insects and rodents. The relation between the average winter survival of each family in F_3 grown in 1927-1928 and F_4 grown in the Agronomy nursery in 1928-1929 is shown in Figure 17. Winterkilling was less severe in 1928-1929 than in 1927-1928; therefore there is considerable range in the survival percentages for the two years. The agreement between the trend of F_3 and F_4 progenies in the thirteen groups in the two seasons is fairly close. Family 136 has a low winter survival each year. Family 135 was above the average in winterhardinesa in both seasons. The results of the

Inheritance of Winterhardiness

Fig. 17 Winter Survival of F_3 Lines and their F_4 Progenies, Kanred x Kanmarg, Agronomy Nursery, (F_3) 1927-28 and (F_4) 1928-29.

artificial freezing trials substantiate the conclusion drawn as to the relative hardiness of these two families in the nursery.

The method of correlation was used in order to get another measure of the relation between winter survival of F_3 and F_4 hybrid rows. The per cent survival of the F_3 row that produced the individual plant used in growing the F_4 row was correlated with the per cent survival of the F_4 row. The distribution of survival percentages for the two generations is shown in Table XXVII. The value of "r" equals .252 ± .0613. This is not high, but is statistically significant. It indicates that there is a positive relation, though not a close one, between the winter-hardiness of F_3 and F_4 progenies. This correlation is probably as high as could be expected, considering the many genetic and environmental factors influencing winter survival. In selecting the individual plants from an F_3 row, there is no assurance that the particular plant selected to produce the F_4 culture is equal in hardiness to the average of the row. In fact in these early generations there are certainly differences between individual plants, as regards winterhardiness. Further segregation probably occurs in many F_4 families.

Table XXVII. Correlation between the survival per cent of F_3 rows and their F_4 progenies, Kanred x Kanmarq, Agronomy Nursery, Manhattan, Kansas 1927-1928 and 1928-1929

F_4 survival per cent	F_3 survival per cent: 62-63.9	64-65.9	66-67.9	68-69.9	70-71.9	72-73.9	74-75.9	76-77.9	78-79.9	80-81.9	82-83.9	84-85.9	86-87.9	88-89.9	90-91.9	92-93.9	94-95.9	96-97.9	98-100	N
60-61.9				1																1
62-63.9																				0
64-65.9											1									1
66-67.9													1				1		1	3
68-69.9																				0
70-71.9															1					1
72-73.9														1	1		1			3
74-75.9																				0
76-77.9				1									2	1	1					5
78-79.9												1	1		1					3
80-81.9										1	1				3		1			6
82-83.9															2				1	3
84-85.9						1				1	1		1		1		1		2	8
86-87.9	1										1				2					4
88-89.9										2					1		1			4
90-91.9																1	3		2	6
92-93.9						1	1			1	1	1		1	3		1		1	11
94-95.9												1	2		2		2			7
96-97.9													1				3		1	5
98-100										2		2	3	4	9		7		8	35
N	1	0	0	2	0	2	1	0	0	7	5	5	11	7	27	1	21	0	16	106

r = .252 ± .0613

A study was made of the F_4 hybrids to determine whether there was a relation between the awn type and winter survival. As is indicated in Table XXVIII., there is no significant difference in per cent survival for the awnless and bearded types.

Table XXVIII. Winter survival of bearded and awnless F_4 types of Kanred x Kanmarq, Agronomy nursery, Manhattan, Kansas, 1928-1929

Awn type	No. of F_4 rows	Average winter survival per cent
Bearded	97	90.3
Awnless	38	91.4
Kanred (bearded)	8	88.5
Kanmarq (awnless)	7	84.6

The awnless rows survived 1.1 per cent more than the bearded rows. A similar study was made in the F_3 generation, and the awnless rows survived only 0.9 per cent more than the bearded types. These differences in winter survival of awnless and bearded types are not considered significant or important.

In order to compare the yields of awnless and bearded types in this cross, the yields of grain in grams per plant were calculated separately for the two awn types in the F_4 population. The number of bearded plants harvested is considerably greater than the number of awnless plants, the numbers being 453 and 99, respectively. The average yield in grams per plant for the awnless and bearded types is given in Table XXIX.

Table XXIX. Yields of bearded and awnless F_4 types of Kanred x Kanmarq, and parents, Agronomy nursery, Manhattan, Kansas, 1928-1929

Awn type	No. of F_4 rows	No. of F_4 plants	Average yield of grain - grams per plant
Bearded	65	453	12.7 ± .1621
Awnless	15	99	10.7 ± .4414
		Difference	2.0 ± .4702 $P.E._{diff}$
Kanred (bearded)		47	10.0
Kanmarq (awnless)		45	10.1

The probable errors of the averages were calculated from the average yield of the plants in each row, rather than from the total number of plants of each awn type. The numbers of rows representing the 453 bearded and 99 awnless plants were 65 and 15, respectively. A

difference of 2.0 ± .470 grams per plant in favor of the bearded plants was obtained. This difference is probably significant though it might be more reliable had the number of awnless types been larger. This result agrees with the results obtained in the F_3 generation, when yields of grain per row were used instead of the mean yields of individual plants. The yields of Kanred and Kanmarq in grams per plant were almost identifal in 1928-1929.

It is generally believed that those plants which produce the greatest yield are better adapted to the conditions under which they are grown and for this reason produce plumper grain of better quality. The correlation coefficient was calculated between the average weight of grain per plant in each row and the average plumpness of the grain produced by these plants. A value of "r" equal to .399 ± .064 was obtained. This value is statistically significant and indicates that the plants which are higher yielding have a tendency to produce plumper grain than the lower yielding plants.

A frequency distribution showing the average plumpness of grain produced by plants harvested from each row is given in Table XXX. The average plumpness of grain for the plants of each family, and the average for all the F_4 hybrids is given in the same table. There is

Table XXX. Distribution of kernel plumpness percentages, F_4 plants of Kanred x Kanmarq, and parents, Agronomy Nursery, Manhattan, Kansas, 1928-1929

Ped. no.	No. of F_4 lines grown	Kernel plumpness, per cent														Average
		59-60.9	61-62.9	63-64.9	65-66.9	67-68.9	69-70.9	71-72.9	73-74.9	75-76.9	77-78.9	79-80.9	81-82.9	83-84.9	85-86.9	
128	2											2				80.0
129	6									1	1	1	3			78.0
130	3							1	2							72.7
131	1							1								75.0
132	13								3	2	5	2	1			76.9
133	2											1	1			81.0
134	4								1	1			2			77.8
135	10		1			1	1		2	1	1	2		1		74.2
136	2											1		1		81.5
137	3										1	1	1			79.7
138	9		1				1		1	2	3		1			74.3
139	14			1				1	1	1	2	3	2	2	1	77.9
140	9							1	1	2	4		1			76.2
Total and average	78	0	2	1	0	1	2	4	11	10	17	13	12	4	1	77.3
	No. of plants															
Kanred	8		1			1		1		2	2	1				74.0
Kanmarq	7	1			1		1	2		1	1					71.0

considerable variation in the plumpness of kernels produced by the different families. Family 136 produced the most plump grain and family 130 the poorest grain. The F_4 hybrids produced grain that averaged higher in plumpness than either the Kanred or Kanmarq parent. The number of parental check rows grown was not large enough, however, to provide a reliable comparison.

The protein content is probably the most reliable indication of quality that can be obtained in small samples of new strains of which sufficient grain for milling and baking tests is not yet available. In order to get some indication of the quality of F_4 rows of the backcrosses, protein determinations were made on 77 samples, through the courtesy of Mr. T. B. Armstrong, of the Kansas State Grain Inspection Department. These protein analyses were made on the bulk seed produced by the F_4 row, not including the grain of the individual plants which had been harvested separately.

An explanation of the material used for these protein studies should be made. Three winter x spring wheats were backcrossed to Kanred, the winter wheat parent. It is these three backcrosses that were used in protein studies. The winter x spring wheats used in these backcrosses were all from the Kanred x Marquis cross. The

F_4 populations of these backcrosses were grown under very similar conditions the same year and in the same section of the nursery. Analyses were made on the bulk seed of 77 hybrid rows, of which 32 lines were Kanred x Kanmarq. The others were Kanred x Tenmarq and Kanred x (Kanred x Marquis). Grain from eight check rows of Kanred and eleven check rows of the winter x spring parents was also analyzed. The distribution of protein percentages of these hybrids and parents and the average protein percentages are given in Table XXXI. The distribution of these lines for protein content is shown graphically in Figure 18. The average protein content of the 77 F_4 hybrid rows was 15.19 per cent, a figure intermediate between the parent varieties. The average protein content of the grain of Kanred was 14.64 and of the winter x spring crosses 16.18 per cent.

The parent varieties differ significantly in protein content. The hybrids are plainly intermediate, with a few reaching the limits set by the parent varieties. These hybrids showed no transgressive segregation for protein content. As can be seen in Figure 18, a leptokurtic curve; i.e. one with a sharp peak, was produced by the distribution of rows for protein content. The mean and modal classes coincide at 15.0 to 15.4 per cent. There is an

Table XXXI. Distribution of protein percentages in F_4 winter x spring backcrosses and parents, Agronomy nursery, Manhattan, Kansas, 1928-1929

	No. of rows	Protein content - per cent								Average
		13.50-13.99	14.00-14.49	14.50-14.99	15.00-15.49	15.50-15.99	16.00-16.49	16.50-16.99	17.00-17.49	
F_4 hybrids	77	7	5	16	26	8	12	2	1	15.19
Kanred	8	1	3	1	2	1				14.64
Winter x spring parents	11			2			4	3	2	16.18

Fig. 18 Protein Content of F4 Winter x Spring Backcrossed Hybrids. Agronomy Nursery, Manhattan, Kansas, 1928-1929.

indication of bi-modality in the curve.

The 32 F_4 Kanred x Kanmarq hybrids and parents were studied separately, and the frequency distributions of protein percentages are given in Table XXXII. These hybrids, even though the numbers are small, agree with the distribution of all F_4 hybrids given in Table XXXI. The hybrids are intermediate between the parents, with no transgressive segregation. A few of the hybrid rows reach the limit set by the parents. Kanred and Kanmarq differ widely in protein content, the percentages being 14.29 and 16.30, respectively. The average of 14.68 per cent protein for the 32 F_4 hybrids is closer to the average of Kanred than of Kanmarq. The presence of a small peak at the right or high side of the curve indicates that hybrid lines are on hand which may have the excellent quality of the Kanmarq parent. Certainly one would be justified in selecting these high protein variants and in studying the protein content of their F_5 progenies.

The distribution of dates of first heading of the F_4 rows of each family is shown in Table XXXIII. A range of five days was found to exist between the average heading dates of F_4 hybrids, grouped according to the 13 original pedigrees. Families 131, 132 and 134 were the earliest, heading on May 28. Families 129 and 138 were the latest,

Table XXXII. Distribution of protein percentages in F_4 Kanred x Kanmarq hybrids and parents, Agronomy nursery, Manhattan, Kansas, 1928-1929

	No. of rows	Protein content - per cent							Average
		13.5-13.9	14.0-14.4	14.5-14.9	15.0-15.4	15.5-15.9	16.0-16.4	16.5-16.9	
F_4 hybrids	32	6	3	8	7	3	3	2	14.68
Kanred	5	1	3		1				14.29
Kanmarq	3						2	1	16.30

Table XXXIII. Distribution of heading dates of F_4 lines of Kanred x Kanmarq and parents, Agronomy Nursery, Manhattan, Kansas, 1928-1929

Ped. no.	No. of F_4 rows	HEADING DATES: MAY 26	27	28	29	30	31	JUNE 1	2	3	4	5	Range	Average heading date
128	3					2		1					3	5-31
129	13					1	3	4	2	2		1	6	6- 1
130	6				1		3	1	1				5	5-31
131	4		2	1			1						5	5-28
132	18	1	3	8	4	1	1						6	5-28
133	5			2	2	1							3	5-29
134	7		2	2	1	2							4	5-28
135	15			1	6	2	4	2					5	5-30
136	3		1			2							4	5-29
137	7			1		2	3	1					5	5-30
138	18				3	4	1	6	2			2	8	6- 1
139	24			5	3	3	6	3	2	1	1		8	5-31
140	16			4	3	1	3	4	1				6	5-30
Totals and averages	139	1	8	24	23	21	25	22	8	3	1	3	11	5-30
	No. of plants													
Kanred	8					1	3	1	2		1		5	6- 1
Kanmarq	7			1	1	1	2	2					5	5-30

heading on June 1. The average heading date of all F_4 hybrids was May 30, the same as for the Kanmarq parent. Kanred headed June 1 or two days later than the average of the F_4 hybrids and Kanmarq. The range of heading dates of F_4 rows of Kanred x Kanmarq is shown in Figure 19. Most hybrid rows are intermediate, with some rows overstepping the limits established by the parent varieties. There appears to be no close relation between the average heading dates of the thirteen groups of F_3 and F_4 hybrids, as can be noted by comparing the average heading dates of F_3 families given in Table XIX. and the average heading dates of F_4 families given in Table XXXIII. This lack of close correlation is not unexpected, because no attempt was made to select for earliness or lateness in F_3. The segregation still taking place for this character may account, in part at least, for the lack of close agreement in heading dates of the F_3 and F_4 generations.

In the fall of 1928 a planting was made at the Colby Branch Station, in northwestern Kansas. Seed from promising plants from the F_3 rows at Manhattan was used to plant these rows at Colby. All of the original thirteen families were represented by two to forty rows. The number of rows planted and the number and per cent of the rows harvested from each of the thirteen original families are shown in

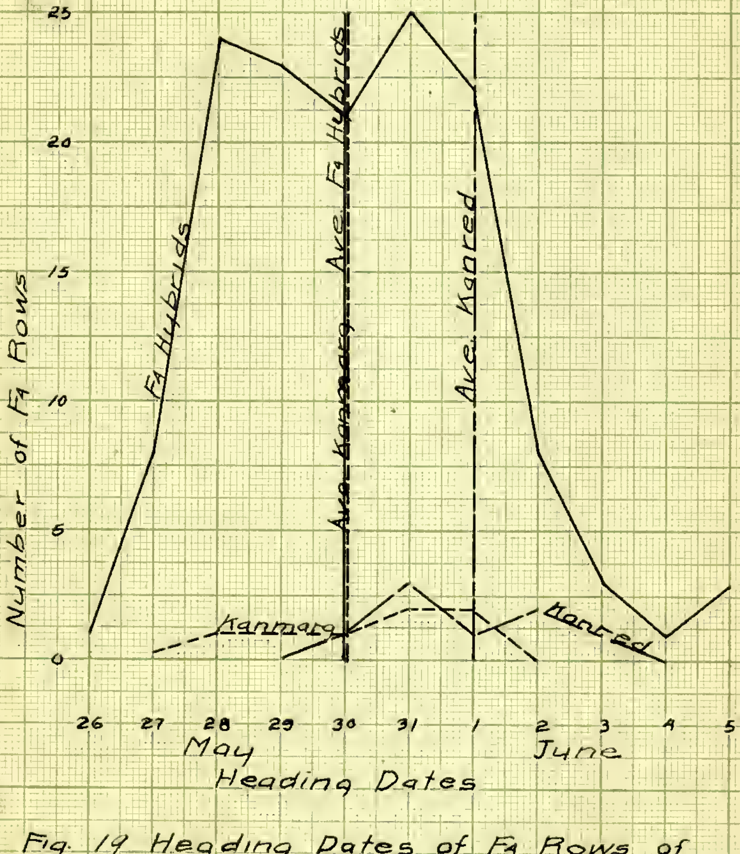

Fig. 19 Heading Dates of F4 Rows of Kanred x Kanmarq and Parents, Agronomy Nursery, 1928-1929.

Table XXXIV.

Table XXXIV. Number of F_4 rows of Kanred x Kanmarq grown and harvested in the nursery at Colby, Kansas, 1928-1929

Pedigree number	No. of rows grown	No. of rows harvested	Per cent of rows harvested
128	9	2	22.2
129	40	4	10.0
130	12	1	8.3
131	13	2	15.4
132	33	4	12.1
133	14	1	7.1
134	17	1	5.9
135	15	2	13.3
136	2	0	0.0
137	18	5	27.8
138	38	2	5.3
139	29	8	27.6
140	30	7	23.3
TOTAL	270	39	

Before harvest, notes were taken on these rows and those that did not look promising were discarded. Rows which appeared more promising were harvested and threshed. It is evident that certain of the original families have the ability to produce more promising lines than others. Conditions at Colby differ widely from those at Manhattan, and for this reason families probably differ in the per cent of desirable rows that they produce at the two

stations. The object of making tho planting at Colby was to obtain some reliable data on tho winterhardiness of these F_4 hybrids, but due to the mild weather of 1928-1929, there was no winterkilling in any of tho rows.

In the fall of 1928 a planting of Kanred x Kanmarq hybrids was also made at Lincoln, Nebraska, through the kind cooperation of Professor T. A. Kiesselbach, for the purpose of studying winterhardiness in the F_4 generation. No winter-killing occurred and no data were obtained on the cold re-aistance of the lines planted there. It was not possible to harveat these rowa at Lincoln, and no notes were obtained.

SUMMARY AND CONCLUSIONS

The cross Kanred x Kanmarq was made in 1923 by Mr. B. B. Bayles, and the F_2 crop grown at Davis, California, in the aeason of 1926-1927. Tho F_3 and F_4 hybrids were grown in the greenhouse and in nuraery rows at Manhattan during the seasons of 1927-1928 and 1928-1929, for the purpose of studying tho inheritance of cold resistance, quality and other characters.

The croas was made for the primary purpose of producing new and superior varieties. The usual agronomic and crop improvement data were taken but no detailed genetic atudies were attempted. It was hoped that a new

bearded variety equal to Kanred in winterhardiness and having the excellent quality and stiff straw of Kanmarq might be produced from this cross. The F_3 and F_4 data indicate that such combinations exist and can be isolated and tested carefully in the next few years.

Newton, Martin, Maximov and several others have studied the fundamental causes of injury due to low temperatures and have made measurable progress in determining the biochemical basis of the differences in cold resistance of varieties of winter wheat. Several theories as to the causes of differences in the cold resistance of wheat varieties have been formulated. The high concentration of the cell sap, and colloids, and the presence of sugars seem to be correlated with cold resistance. The higher the osmotic pressure and the more bound water, the more hardy the plant.

Nilsson-Ehle, Hayes, Martin, Quisenberry and Clark, and others have studied the inheritance of winterhardiness but have been unable to determine the specific genetic factors governing cold resistance. This character is evidently quantitatively inherited, and most hybrid populations are intermediate.

Inheritance of quality in wheat has been studied by Hayes and Bailey, Clark and others. Quality is a very

complex character, quantitatively inherited, and is certainly influenced by several factors. Most crosses have given hybrids of intermediate quality, with occasional transgressive segregation.

The F_3 generation of the Kanred x Kanmarq cross was studied by growing two large populations in the greenhouse, and one of 201 space-planted rows in the crop improvement nursery, during the winter of 1927-1928.

The plants in one of the greenhouse plantings were moved outside and exposed to natural outdoor conditions when the plants were seventeen days old. Two severe cold spells caused almost complete killing of the hybrids and parent varieties. The parent varieties had a [illegible] higher survival than the hybrids. The results of this outdoor freezing test are of doubtful value, because of the very severe injury to young, unhardened plants of both parents and hybrids.

Plants in the other greenhouse planting were artificially frozen in the refrigeration machine in the greenhouse. Freezing was started when the plants were seventy-five days old. Plants were subjected to temperatures of approximately -10.0° C. for twelve hours.

In this freezing test the hybrids showed the least injury, 49.9 per cent. Plants of the Kanred and Kanmarq

parents were injured 63.1 and 72.2 per cent, respectively, on the average. These data indicate that the hybrids, on the average, are more resistant than Kanred, the more winterhardy parent.

Differences in freezing injury to plants frozen during the day and at night were very striking. Kanred, Kanmarq and their F_3 hybrids were injured 83.9, 91.1 and 71.2 per cent when frozen during the day. When frozen at night the freezing percentages of similar material were as follows: 46.5, 59.1 and 32.9, respectively. This difference in injury to plants frozen during the day and at night may be explained by the fact that during the day sugars are stored in the tissues, the concentration of the cell sap is increased and the plants are made more resistant to the freezing given during the night. On the other hand, at night the sugars are used up and a decrease in the cell sap concentration lowers the cold resistance of plants frozen during the daytime after a twelve-hour period of darkness and photosynthetic inactivity.

Freezing of plants caused a delay of from five to fifteen days in heading of the parent varieties and hybrids.

No relation was found between cold resistance and awn type, either in artificial freezing studies or in field tests.

Bearded types yielded significantly more than the awnless types in the F_3 and F_4 generations.

The F_4 crop was studied in the greenhouse and in eight-foot, space-planted rows in the nursery in 1928-1929. The method of freezing the F_4 hybrids in the greenhouse was changed from that used for the F_3 generation. A freezing time of six hours with temperatures of 12° F. was used. Lower temperatures and shorter time were used in F_4 than in F_3. Plants frozen in the morning and in the afternoon reacted in a manner closely resembling those of the F_3 generation frozen during the day and at night.

Both field and greenhouse freezing trials with the F_4 hybrids show that they are more hardy than either parent. In both greenhouse and field freezing trials, Karmarq showed less resistance to cold than Kanred. This is in agreement with field observations on these two varieties.

The F_3 hybrids grown in the field were intermediate between the parents in winter survival, while the F_4 hybrids had a higher per cent of winter survival than either parent. This suggests that progress was made in selecting F_3 plants that were resistant to cold, thereby increasing the average cold resistance of the F_4 population.

A correlation coefficient of .252 ± .061 was obtained

between the per cent winter survival of the F_3 plants and their F_4 progenies. This value is probably as high as could be expected in these early generations, considering the complicated nature of winterhardiness, and the many factors affecting it.

Protein content of grain from the F_4 hybrids was intermediate between the parents with no evidence of transgressive segregation.

There is evidence that bearded types have been isolated from the backcross, Kanred x Kanmarq, which combine the excellent quality and stiff straw of Kanmarq with the winterhardiness of Kanred.

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